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E. E. GREEN, Way's End, Camberley (late Government Entomologist, Ceylon)

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CONTENTS OF VOL. VII, No. 1

		PAGE
1.	On a New Polyembryonic Encyrtid (Chalcidoidea) *Copidosoma Tortricis* sp. N. Bred from the Strawberry Tortrix Moth. By JAMES WATERSTON, B.D., B.Sc. (With 5 Text-figures)	1
2.	The Life History of the Strawberry Tortrix, *Oxygrapha comariana* (Zeller). By F. R. PETHERBRIDGE. (With Plate I)	6
3.	Daily Periodicity in the Numbers of Active Soil Flagellates: with a brief Note on the Relation of Trophic Amoebae and Bacterial Numbers. By D. WARD CUTLER and L. M. CRUMP. (1 Map and 7 Text-figures)	11
4.	Spartina Problems. By Prof. F. W. OLIVER, F.R.S. (With Plate II and 3 Text-figures)	25
5.	Investigation of the Nature and Cause of the Damage to Plant Tissue resulting from the Feeding of Capsid Bugs. By KENNETH M. SMITH, A.R.C.S., D.I.C. (With Plate III and 5 Text-figures)	40
6.	*Sphaeronema* sp. (Mouldy Rot of the Tapped Surface). By A. R. SANDERSON, F.L.S. and H. SUTCLIFFE, A.R.C.S. (With Plates IV–VII)	56
7.	The Habits of the Glasshouse Tomato Moth, *Hadena* (*Polia*) *oleracea*, and its Control. By LL. LLOYD, D.Sc. (With Plates VIII–X and 4 Diagrams)	66
8.	A Quantitative Analysis of Plant Growth. Part I. By G. E. BRIGGS, M.A. (Cantab.), FRANKLIN KIDD, M.A. (Cantab.), D.Sc. (Lond.) and CYRIL WEST, A.R.C.Sc., D.Sc. (Lond.). (With 9 Text-figures)	103
9.	Notes on Chemotropism in the House-Fly. By E. R. SPEYER	124

VOLUME VII SEPTEMBER, 1920 No. 1

ON A NEW POLYEMBRYONIC ENCYRTID (CHALCIDOIDEA) *COPIDOSOMA TORTRICIS* SP. N. BRED FROM THE STRAWBERRY TORTRIX MOTH.

BY JAMES WATERSTON, B.D., B.Sc.

(Published by permission of the Trustees of the British Museum.)

(With 5 text-figs.)

DURING the course of investigations into the life history of the Strawberry Tortrix (*Oxygrapha comariana* Z.) in 1918 and 1919, of which the results appear elsewhere (p. 6), Mr F. R. Petherbridge reared a small chalcid in numbers and was good enough to send me some of his material for study. With the hymenoptera there were fortunately enclosed two of the irregularly swollen dried skins of the hosts whose remarkable appearance (Fig. 1) at once suggested a polyembryonic

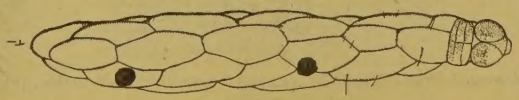


Fig. 1. Larva of *Oxygrapha comariana* Z., showing the characteristic swellings produced by the pupation of *Copidosoma tortricis* Wtrst. with holes of emergence of the parasite.

method of reproduction on the part of the parasite. Although Mr Petherbridge could supply no direct evidence on this point he had made the significant note that as many as 35 of these parasites might emerge from one larva.

Having dissected and thoroughly examined both sexes of the chalcid I came to the conclusion that it should be assigned to the genus *Copidosoma* Ratz. but neither the named material in the British Museum collection—at present in an unsatisfactory state—nor a study of Mayr's Monograph of the European Encyrtidae enabled me to determine the species. Recently I have submitted both dried specimens and various preparations of the *Copidosoma* to my friend Prof. F. Silvestri who, however, can suggest no definite name for the insect though he knows

it well, having reared a practically identical form from a *Tortrix* sp. in Italy. As Prof. Silvestri tells me he has found this *Copidosoma* to be polyembryonic in Italy I have no doubt the British form is so too.

Superfamily: CHALCIDOIDEA.

Family: ENCYRTIDAE.

Genus: **Copidosoma** Ratzeburg (1844).

Copidosoma tortricis sp. n.

Distinguished by the proportions and chaetotaxy of the antennae (♂, ♀) (Fig. 3 *a*, *b*) especially by the short second funicular joint (♂); the proportions of the head (Fig. 2 *b*); labrum (Fig. 2 *c*); and radius (Fig. 5). The colour of the antennae is probably also of importance.

Note. The proportions of the antennal joints must be studied in properly prepared mounts. In naturally dried specimens there is considerable distortion and the club (♀) in particular is liable to appear unduly flattened. The filamentous end of the preapical dorsal mandibular bristle (Fig. 2 *a*) is often broken off.

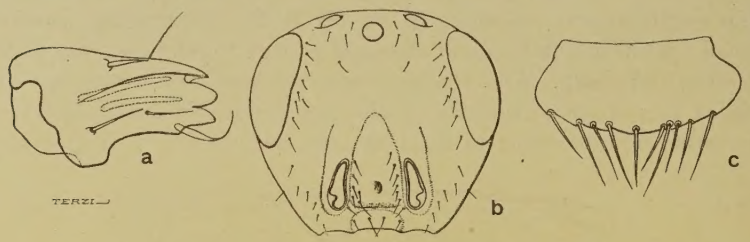


Fig. 2. *Copidosoma tortricis* Wtrst. ♀. (*a*) right mandible from inside, (*b*) head from in front, (*c*) labrum.

A dark blackish brown species in both sexes, with metallic reflections on head and thorax and submetallic on the abdomen dorsally.

♀. Reflections variable but mainly as follows. On face, frons, vertex, pronotum and scutum mainly dark green or aeneous green; on scutellum and mesopleurae (more shining) and abdomen (more dully) purplish. Outer aspect of hind coxa submetallic.

Antennae concolorous, blackish brown. Palpi paler than rest of trophi. Wings sub-hyaline very faintly and uniformly tinted; neuration brownish, indistinctly and shortly clouded at the base of the radius distally. Legs all tarsi paler, fore and hind coxae, trochanters, femora (except the extreme apex), tibiae (except for a narrow basal ring and in the fore pair sometimes the tip obscurely) blackish—the excepted portions paler. In the mid legs the coxa is dark, trochanter, base of tibia (narrowly) and apex (more broadly) paler. The main portion of the mid femur is brown, not nearly so dark as the fore or hind femora. Mid tibiae variable—as pale as the fore tarsus with an indistinct darker dorsal streak.

♂ similar to the ♀ in colour but with definitely darker legs in which the knees, tarsi and sometimes the apex of the fore tibia (obscurely) alone are paler.

♀. Head (Fig. 2 *b*), just broader than long (13 : 12). Eyes rather short and little more than half (5 : 9) the length (depth). Frons very wide, the eyes at the level of the anterior ocellus separated by about $\frac{1}{2}$ and on the base line by $\frac{7}{8}$ of the breadth. Malar space large, the malar impressed line $\frac{4}{5}$ the depth of the eye or barely half (4 : 9) that of the head. Toruli elongate, much longer (12 : 5) than broad; distant from the clypeal edge at $\frac{1}{2}$, and from one another rather over, their own length. Besides the usual short bristles along the orbits frontally, there are two (1 : 1) minute, below the anterior ocellus, 6–7 on each side between the toruli and 4 (1 : 2 : 1), stronger on the clypeus, remote from the edge. The intertorular area is somewhat tumescent. Pattern moderate, regular, distinctly but not strongly raised.

Antenna (Fig. 3 *b*). Length about 1 mm., scape and bulla together not quite half as long as the remainder of the antenna. Scape (6 : 1) nearly thrice the pedicel (7 : 4) longer than the first four joints of the funicle and about $\frac{1}{4}$ longer than the club.

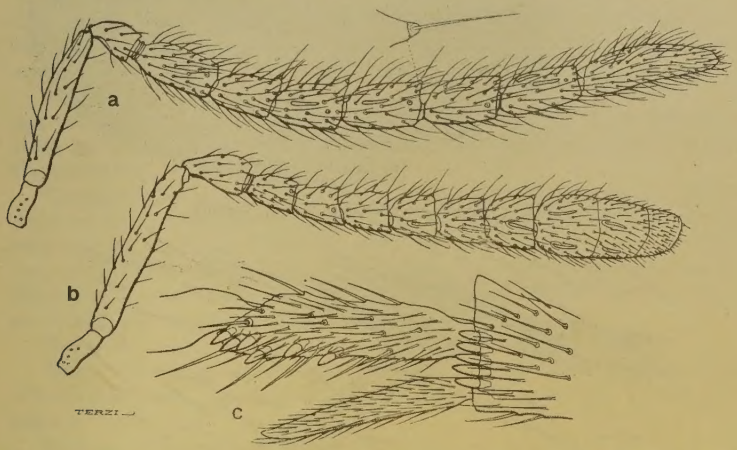


Fig. 3. *Copidosoma tortricis* Wtrst. (*a*) Antenna ♂, (*b*) antenna ♀, (*c*) first joint of mid tarsus and apex of tibia ♀.

Funicle expanding from the second joint onwards, sixth joint nearly as wide as the club and much broader (7 : 4) than the first, but only a little longer (9 : 8). The insertion of the funicular joints is infra median and the distal superior angle is indistinctly produced and setigerous. The club is distinctly segmented only on one side and the sensoria are few. Labrum (Fig. 3 *c*), mandibles (Fig. 3 *a*) elongate, tridentate, maxillary palpus 12 : 10 : 15 : 25. Last joint with four stouter bristles (1 median, 2 preapical, and 1 apical) at the edge (of which the last is $\frac{2}{3}$ the joint) and 14–16 finer over its surface. Labial palpus 12 : 15 : 12, apical bristle as long as the joint which bears 6–7 in all.

Thorax and propodeon subequal, both in length and breadth to the abdomen, but broader than the head. Thorax + propodeon + head shorter than antenna.

Pronotum, posterior row of about 18 bristles. Prosternum twice as broad as long. Prepectus entirely reticulate. Tegulae three bristles. Axillae not quite touching, with

one minute bristle. Scutellum, about $\frac{1}{6}$ shorter than the scutum with about 30 bristles. Propodeon extremely short spiracle small, broadly oval, situated at the extreme side where the segment is intumescent and posteriorly angulate. One or two pleural bristles and another small patch of the same behind the spiracle, the individual bristles rising from minute wart-like excrescences.

Wings, forewings (Fig. 4) (7 : 3) length 1·3 mm., on the submarginal vein 12–14 bristles. Radius (Fig. 5) with a single bristle and four terminal pustules, on the dorsal surface along the edge of the submarginal cell are about 30 bristles. Below

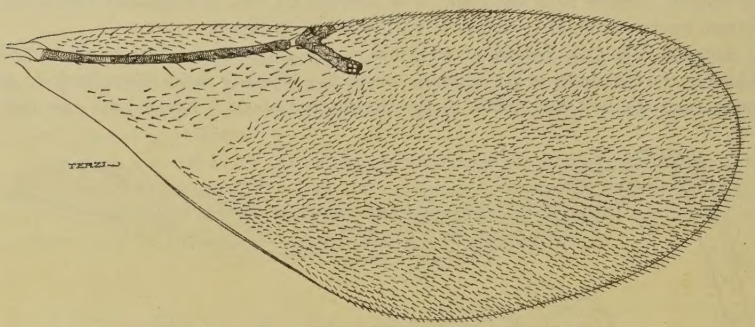


Fig. 4. *Copidosoma tortricis* Wtrst. ♀ wing.

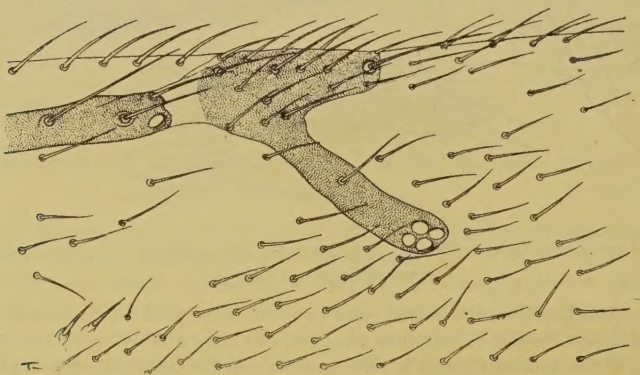


Fig. 5. *Copidosoma tortricis* Wtrst. ♀. Details of radius of wing.

nearly the whole surface of the cell is covered with bristles of which about 10 towards the apex are longer and oblique. There are 6–8 rows of bristles basally before the "hairless streak." Hind wings (7 : 2) length ·8 mm. Forelegs, femur equal to tibia. The latter with comb of six rather long spines apically. Upper apical angle of tibia with one chitinous tooth anteriorly and another posteriorly, first tarsal comb of 12 spines. Proportions of first three tarsal joints, 9 : 6 : 5.

Mid leg, femur shorter (6 : 7) than tibia. Spur of the latter shorter than first tarsal joint (Fig. 3 *c*). Heavy spines on apex of tibia 5, on tarsus 6, 4, 4, 2, 0, respec-

tively. Tarsus, 14 : 7 : 6. Hind legs, femur shorter (5 : 6) than tibia, comb of the latter 10 spines, longer spur $\frac{5}{6}$ of the first tarsal joint, second very short about $\frac{1}{4}$ of the first. Tarsus 12, 8, 7.

Abdomen. Along the mid line the first tergite exceeds all except the seventh, which is slightly longer, 2–4 and 6 are subequal, 5 longer. Setigerous process half as broad again as long, with 3 long and 1 shorter seta. Distance between the processes greater (3 : 2) than the longest seta or (3 : 1) than the distance from either process to the spiracle. The latter minute, circular, 12–14 bristles distally on spiracular overlap. Pattern of abdomen raised and coarser anteriorly on first tergite, smoother posteriorly and medianly. Terebra distinctly shorter than its sheath. Distal portion of the latter ($\frac{2}{3}$ the base) with one bristle. 3–4 bristles apically on the pleural flap above.

Length 1·3 mm.

Alar expanse, 3 mm.

♂. Head, broader than long (nearly 5 : 4) much broader relatively than in ♀. The base line of the eyes cuts off the upper $\frac{1}{4}$ of the toruli. The latter at their nearest separated by more than, and from the clypeal edge by $\frac{2}{3}$ of, their own length.

Antenna (Fig. 3 *a*), length 1·1 mm. Scape over thrice the pedicel equal to the first two and $\frac{1}{3}$ of the third funicular joints together. Funicle of practically equal width but widest on the third joint with the unsegmented club tapered apically. The second joint is the shortest.

Throughout the antenna bears numerous moderately strong fuscous bristles which are more or less curved apically. At the upper distal angle (in profile) of each funicular joint and about the middle of the dorsal edge of the club is a tubercle (very conspicuous on joints 2–4) emitting a single characteristic fine *hyaline* bristle. Being neither coloured nor apically curved, these bristles in spite of their fineness are exceedingly conspicuous. There are few sensoria.

Thorax and propodeon together shorter than abdomen.

Wings. Forewings a little over twice as long as broad, about the same length (1·3 mm.) as in the ♀ but broader. Hind wings slightly more (22 : 7) than three times as long as broad.

Forelegs, tibia just shorter than femur.

Abdomen, tergite 7 longest—half as long again as 1.

Last sternite apically broadly emarginate. Genitalia. Basal plate with 6–7 bristles on each side. Paramer bidentate, rather slender, about $\frac{2}{3}$ the breadth of the plate in length.

Dimensions much as in ♀ the abdomen however slightly longer.

Type ♀ in Brit. Mus. one of a series (♂, ♀) bred from larva of *Oxygrapha* (*Peronea*) *comariana*, Z., England, Cambridge, Summer 1918 and 1919 (F. R. Petherbridge).

(The figures illustrating this paper are reproduced by permission of the Ministry of Agriculture.)

THE LIFE HISTORY OF THE STRAWBERRY TORTRIX, *OXYGRAPHA COMARIANA* (ZELLER).

By F. R. PETHERBRIDGE.

School of Agriculture, Cambridge.

(With 1 Plate.)

The first record of serious damage by the caterpillars of this moth was made by Miss Ormerod[1], from notes sent by Dr Ellis of Liverpool in 1883, who in turn recorded them from Mr Richard A. Wrench, of Dee Banks, Chester. The strawberries attacked were in the neighbourhood of Dee Banks.

The next record is by Theobald[2] who records them as doing serious damage to a field of strawberries belonging to Messrs G. Mount and Sons.

From 1913–1917 they caused serious damage to strawberries at Terrington St Clements, Walpole and Walton between King's Lynn and Wisbech, and in several cases reduced the crop to about 25 per cent. of a normal one, with the result that many acres of strawberries were ploughed up as being unprofitable. In 1918 they were recorded by Theobald as present in Warwickshire, Somerset and Hertfordshire.

Life History. The young larvae begin to hatch out at the end of April or early in May. In 1918 they were found on April 21st, but in 1917 and 1919 they were not found until the first week in May. As soon as they hatch they begin to feed on the very young folded fan-shaped leaves and to make holes through the successive layers: sometimes they leave the upper epidermis intact. They remain sheltered by the folded leaves so that they are not visible until the leaves are unfolded. After a time some of the larvae begin to feed on the unopened flowers. They bore a hole through the folded calyx and feed on the stamens and developing carpels, with the result that the flowers attacked either do not form fruit or form only distorted ones.

[1] Ormerod, E. A. *Handbook of Insects Injurious to Orchard and Bush Fruits*, pp. 258–260.

[2] *The Journal of the South-Eastern Agricultural College*, 1911.

The caterpillars bind the leaflets, and often several leaves together, by means of threads, this providing an easy means of recognising an attack. They also make little webs on the backs of leaflets under which they feed and moult. They can crawl fairly quickly, and when touched they wriggle in the characteristic tortrix manner. Sometimes they suspend themselves from the plants by means of long threads.

The caterpillars hatch over a fairly long period and remain feeding until nearly the end of June (June 29th in 1916; June 15th in 1917; June 25th in 1918).

Pupation takes place in the webs on the leaves which have been spun together, i.e. where the larvae have been feeding. It usually starts early in June, but may take place at the end of May (May 23rd, 1911, Theobald; June 1st, 1917; June 11th, 1918).

The moths begin to hatch out in June (June 7th, 1911, Theobald; June 21st, 1917) and may be found up to the end of July. They may be found sitting on the leaves or crawling about in the centre of the plants, and may often be seen to fly short distances when disturbed. Apparently they are not capable of flying far, as the attack has spread very slowly. Fields adjoining others badly attacked remained free from attack for two years. This first brood of moths lay their eggs during July usually on the backs of the stipules at the base of the plant, but occasionally on the lower part of the leaf stalks. Moths brought from Walton on July 11th, 1917 were put on strawberry plants in a breeding cage. Young caterpillars were first found on July 21st. Caterpillars were found at Walton on July 18th and also at intervals until September 5th.

Pupae were found on August 19th, 1917 and until September 20th. Moths were found on September 11th and were present until November 17th. After this date no moths were found until the following June. Several observers suggest that the moth hibernates. Theobald says[1] "The moths apparently hibernate, for I have taken them by beating in late October at Buxton and again in the early spring at Wye."

Although I searched carefully for these moths during the winter and spring I found none from December to June, and I came to the conclusion that the moths do not hibernate. Moreover a large number of eggs were present on the plants from November onwards. This has an important practical bearing, for by ploughing up a piece of strawberries in December, the eggs will almost certainly be prevented from giving rise to moths next spring.

In 1917 a few eggs were first found on the stipules on November 3rd

[1] Theobald, *Insect Pests of Fruit.*

and they gradually increased in number until the middle of the month. Most of the eggs in 1917 were laid during the first half of November, as during that time numbers of eggs were laid in the boxes in which the moths were brought from Walton. In 1918 eggs were found on October 25th, but owing to the scarcity of moths due to the killing of the larvae by Chalcid parasites, it was difficult to tell how long the moths lived. None were found after the middle of November.

Two moths were found about two feet from the ground on some sticky bands on apple trees near which some strawberry plants had been heeled in.

The following table shows the life history of the pest in 1917. This seems to be a fairly normal one, but there are seasonal variations as mentioned above.

Stage	When found	Length of life of the various stages
Caterpillar	Beginning of May—middle of June	4–5 weeks
Pupa	During June	2–3 ,,
Moth	Last week in June—end of July	4 ,,
Egg	Last three weeks of July	1 week
Caterpillar	Mid July—beginning of September	4–5 weeks
Pupa	Third week in August—end of third week in September	2–3 ,,
Moth	Second week in September—third week in November	about 8 ,,
Egg	Beginning of November—middle of May	about 6 months

The eggs are laid singly usually on the outside of the stipules, but occasionally on the lower part of the petioles. Two or three eggs may be present on one stipule.

The egg is very flattened, and broadly oval in outline, measuring 0·86–0·96 mm. in length and 0·64–0·69 mm. in breadth. The shell of the egg is of a silvery white colour, beautifully sculptured, being covered all over with a raised network which is best seen round the edges while the developing larva is still present (Pl. I, fig. 1). The developing larva is at first yellowish, but later assumes a reddish orange colour. The egg is easily seen owing to the whitish rim of the shell which extends beyond the developing larva.

The larva varies according to its stage of development, so much so, that at first I thought I was dealing with two different species.

In the young larval stages the head and the first thoracic plate are shining black, but in the older stages they are yellowish.

I watched a larva about 6 mm. long, with a black head and thoracic plate, in the process of moulting, and found that the head and thoracic plate of the remaining larval stages remained yellow.

On hatching it measures 1·9–2·1 mm. and when full grown 9·5–11 mm. in length. In the young larval stages the body is of a dirty white or dirty yellow colour and the short legs are brownish black, except at their bases, which are greenish. The head and body are hairy as in the later stages (see Pl. I, fig. 2).

In the older stages the head is yellowish, semi-transparent, with light brown splashes on the vertex, and with a pair of black spots on each side, which are not visible when the caterpillar is looked at from above. The anterior of these spots is situated just behind and below the antenna and round the group of eyes. The posterior one is situated at the same level near the posterior margin (see Pl. I, fig. 2).

The first thoracic plate is of a pale yellowish colour in those larvae which have a yellowish head. These later stage larvae have legs of a yellowish brown colour.

The body is at first of a dirty white or dirty yellow colour, but later on may be either a dull yellowish green, a yellowish brown or a dull green colour.

The dorsal vessels appear as a dark green line down the middle of the body and can be seen pulsating. On each side of it is a sub-dorsal line of a dark colour.

The pupa is 6·5–7·5 mm. in length and very variable in colour. At first the head is brown, the wing cases green and the abdomen brownish yellow; but later on the green colour usually disappears and the wing cases become yellowish brown and the abdomen reddish brown.

The moths are also very variable in colour. The triangular patch on the fore wing may be of a rich brown colour or almost black.

Parasitism. In 1918 both broods of caterpillars were badly parasitised by the larvae of a small Chalcid[1]. As many as 35 Chalcids were reared from a single caterpillar. The larvae eat the inside of the caterpillar and leave only the skin. The outline of each larva can be seen through the transparent skin. They cause the skin to bulge. The first brood of adult chalcids appears in July, and although I found chalcid pupae in October I have no record of the date of appearance of the second brood of adults. A single pupa was found containing a large hymenopterous parasite, but this did not mature.

Remedial measures.

In 1918 I tried the effect of spraying attacked plants with Lead Arsenate and with powders containing Calcium Arsenate and Calcium

[1] A description of the parasite is published on p. 2 of this number of the *Journal*.

Arsenite respectively. These sprays did not succeed in reducing the caterpillars to any extent, probably due to mechanical difficulty of reaching with the spray the young folded leaves on which the young caterpillars feed.

Many of the growers who sprayed with Lead Arsenate were pleased with the results, but they were then probably not aware that, thanks to the energies of the chalcid parasites, the caterpillars had almost disappeared from strawberries which were not sprayed.

Apart from parasites, the best means of reducing this pest seems to be to run a mowing machine over the crop so as to cut off the tops as close to the crown as possible when the pest is in the second pupal stage, viz. at the beginning of September. (It is a common practice with many growers to cut off the tops during the autumn.) The tops must then be raked up and burnt or buried before the moths come out, i.e. the middle of September. I tried this on one field but unfortunately the grower waited too long before destroying the tops. (NOTE: the eggs are laid too low down to be cut off in this manner.)

Old strawberry beds destined to be ploughed up should be ploughed after the eggs are laid in November, as by ploughing earlier than this the moths will probably lay their eggs on neighbouring crops of strawberries, or on wild plants of Fragaria and Comarum near.

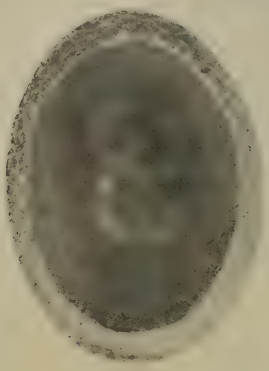


Fig. 1. The egg of *Oxygrapha comariana* (× 56).

Fig. 2. Late stage larvae of *Oxygrapha comariana*.

Fig. 3. *Oxygrapha comariana* (after Theobald).

DAILY PERIODICITY IN THE NUMBERS OF ACTIVE SOIL FLAGELLATES: WITH A BRIEF NOTE ON THE RELATION OF TROPHIC AMOEBAE AND BACTERIAL NUMBERS.

By D. WARD CUTLER and L. M. CRUMP.

(*Rothamsted Experimental Station.*)

(1 Map and 7 text-figs.)

In a recent paper by one of us (4) are given the results of periodical counts of the protozoa found in certain of the Rothamsted fields. These numbers refer, however, to the total protozoan population irrespective of their physiological conditions—cystic or trophic. A method (6) has recently been devised by which these two states can be separated and the numbers counted. From October 8th, 1919 to January 29th, 1920 fortnightly soil samples were taken from the dunged plot of Rothamsted wheat field and the trophic and cystic protozoa counted.

Fig. 1 gives the active numbers per gr. of soil for three species of flagellates (*Oicomonas* sp. (Martin), *Cercomonas longicauda*, Bodo sp.), the numbers of trophic amoebae and the bacterial numbers. On the same curve is also given the moisture content of the soil. Fig. 2 shows the curves for the daily rainfall and soil temperature 1 ft. depth (Meteorological Office type thermometer) during the period.

Examination of these curves suggests no correlation between the number of active organisms and the temperature or water content, but there is an indication of periodicity in the fluctuations of numbers of active flagellates. The sudden rise in numbers on Nov. 13th is probably due to addition of manure to the soil seven days previously. It is interesting to note, however, that this did not prevent cyst formation and subsequent reduction in active numbers on Nov. 25th.

As the soil samples were taken at approximately fortnightly intervals the figures give no information as to the daily fluctuations in number of the protozoa—obviously a matter of great interest; to determine this daily samples were taken from the Broadbalk dunged plot—the first on Feb. 9th, 1920.

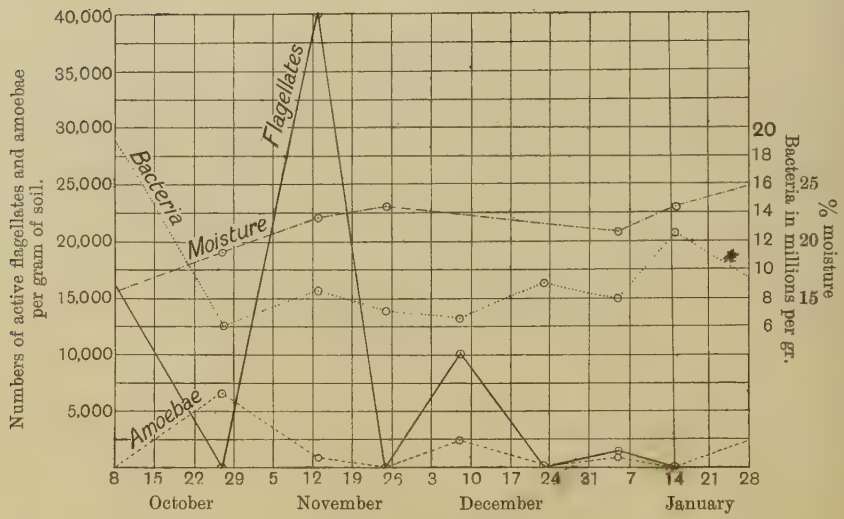


Fig. 1. Numbers of active flagellates, amoebae and bacteria per gramme of soil and percentage of moisture in Broadbalk, plot 2, from October 8, 1919—January 28, 1920. Bi-monthly countings.

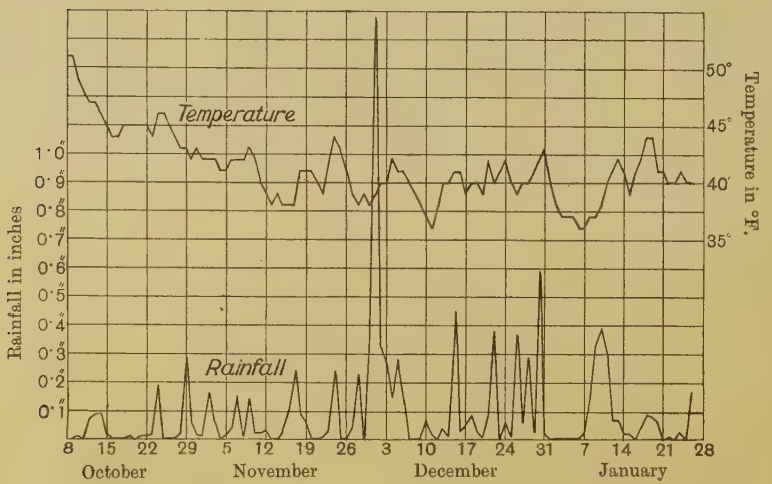
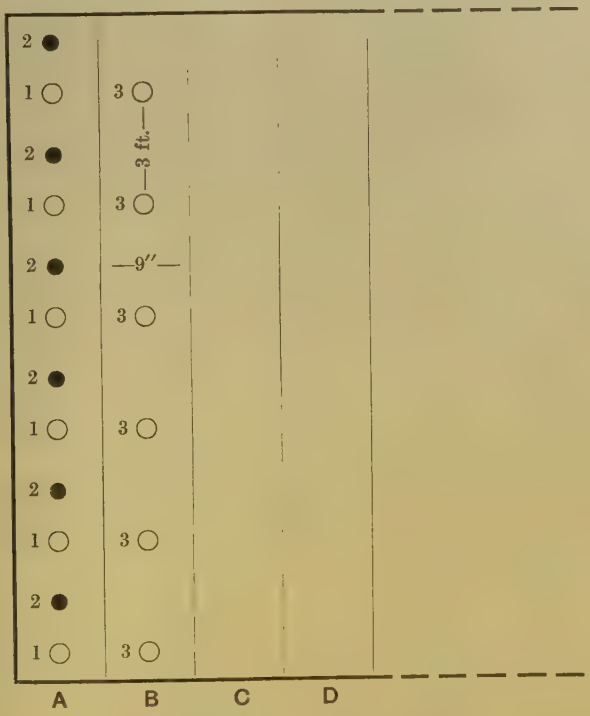


Fig. 2. Rainfall and ground temperature from October 8, 1919—January 28, 1920.

METHODS.

The method of sampling was as follows: In the centre of the plot 14 rows between the young wheat plants were selected. Four of these—A, B, C, D—are shown in the accompanying map.

Six 9-inch borings, taken at intervals of about 3 ft. along row A, and thoroughly mixed together formed sample 1, which was taken to the laboratory in a sterile bottle.



Map showing method of taking samples.

The second sample was taken the following day in the same way as the first, except that the borings were taken between those of the previous day.

The samples for the third and fourth days were taken in the same manner as the sample for the first and second, but from row B. In this way 28 samples were obtained from 14 rows of the plot. The counting

method employed is a dilution one, fully described in a recent paper (6). Briefly, it consists of dividing the sample into two 10 gr. portions. One of these is made up into a series of suitable dilutions, from each of which 1 c.c. is inoculated on to agar plates which are incubated at 18° C., and examined at 7 and 14 day intervals. If, for example, growth occurs in the 1/1000 dilution plates there was at least one organism producing this growth, and it is assumed that there are at least 1000 per gr. of soil. Thus by using dilutions sufficiently near to one another the total number of protozoa per gr. of soil can be ascertained. To find the number of active forms the second 10 gr. portion of the soil is treated overnight with 2 per cent. HCl; this kills all active forms leaving the cysts uninjured. The number of protozoa in this treated sample subtracted from that in the untreated gives the number of active protozoa per gr. of soil. Proof of the accuracy of this method is given in the paper referred to above, and further proofs are annexed on pp. 14 and 16 of the present paper.

RESULTS OF DAILY COUNTS.

The daily numbers of active and cystic forms of the three species of flagellates are given in Table I and Figs. 3 and 4. It will be seen that the total numbers—trophic and cystic—exhibit great fluctuations, rarely being the same for two days together. The most remarkable feature presented by the results, however, is the wholly unexpected daily periodicity in the fluctuation in numbers of the trophic forms. We think there is no doubt as to the reality of this periodicity.

Table I. *Giving the total—cystic and active—numbers per gr. of soil for three species of flagellates on successive days, beginning February 9th and ending March 8th*, 1920.

Day	Total	Cystic	Active	Day	Total	Cystic	Active
1	9,000	5,000	4,000	15	15,000	3,250	11,750
2	6,000	6,000	0	16	15,000	6,500	8,500
3	9,000	3,250	5,750	17	15,000	3,000	12,000
4	2,500	1,800	700	18	6,500	6,500	0
5	6,500	2,500	4,000	19	20,000	1,000	19,000
6	5,000	5,000	0	20	7,500	3,250	4,250
7	9,000	600	8,400	21	9,000	2,500	6,500
8	5,000	2,500	2,500	22	6,500	2,500	4,000
9	5,000	1,000	4,000	23	15,000	3,250	11,750
10	1,500	1,000	500	24	5,000	3,250	1,750
11	9,000	1,000	8,000	25	10,000	1,500	8,500
12	6,500	3,250	3,250	26	5,000	2,500	2,500
13	15,000	1,000	14,000	27	6,500	1,000	5,500
14	10,000	6,500	3,500	28	25,000	25,000	0

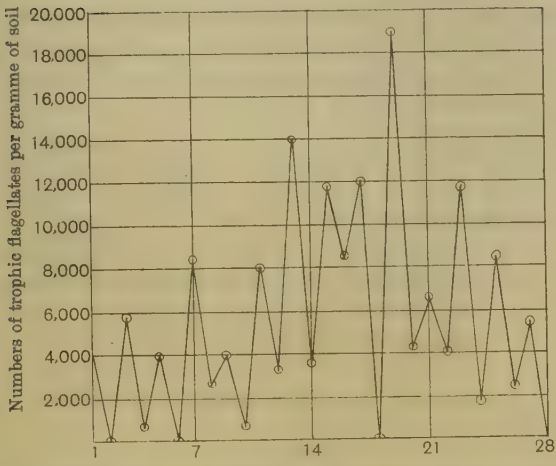


Fig. 3. Active flagellates in Broadbalk, plot 2, from February 9—March 8, 1920. Daily countings.

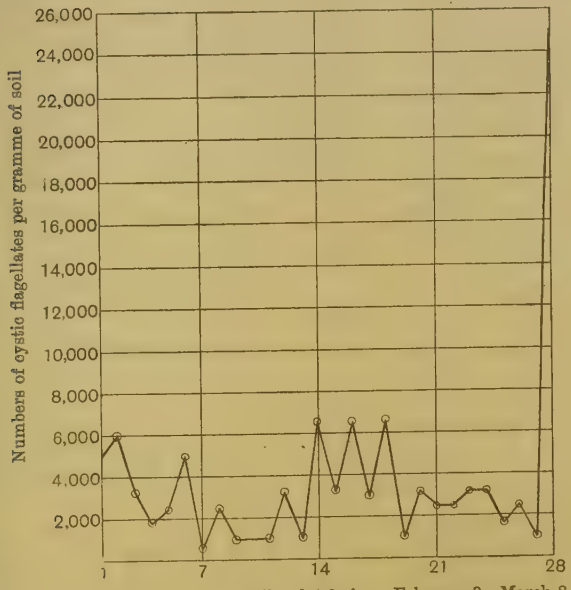


Fig. 4. Cystic flagellates in Broadbalk, plot 2, from February 9—March 8, 1920. Daily countings.

The regularity of the alternation is evidence of the reliability of our methods; for it is almost impossible to believe in an experimental error having so constant and so distinct a rhythm.

The possible sources of error are:

1. Method of counting.
2. Uneven distribution of protozoa in the field.
3. The death of cysts as well as of active protozoa by the use of 2 per cent. HCl.

Method of Counting. The paper in which this method is described (6) gives proof of its accuracy; a few further examples may, however, be given.

Table II.

	Amoebae		Flagellates		Ciliates	
	Active	Cystic	Active	Cystic	Active	Cystic
1. Number organisms added	40,000	25,000	100,000	100,000	5,000	32,500
„ „ after treatment		25,000		95,000		30,000
2. Number organisms added	50,250	96,800	130,000	560,000	35,000	10,000
„ „ after treatment		95,000		500,000		10,000
3. Number organisms added	20,000	15,000	90,000	45,000	35,000	15,250
„ „ after treatment		12,500		40,000		10,000
4. Number organisms added	4,000	2,500	6,500	1,500	5,000	25,400
„ „ after treatment		2,000		1,000		20,000
5. Number organisms added	537,000	645,000	1,500	1,000		
„ „ after treatment		600,000		900		
6. Number organisms added	30,000	50,000	250,000	100,000	2,500	5,000
„ „ after treatment		45,000		85,000		4,000
7. Number organisms added	50,250	40,000	50,000	250,000		
„ „ after treatment		35,000		200,000		
8. Number organisms added	10,000	5,000	20,000	2,500		
„ „ after treatment		4,500		2,000		
9. Number organisms added	12,500	35,000	15,000	100,000	25,000	1,000
„ „ after treatment		32,500		85,000		1,000
0. Number organisms added	150,000	10,000	250,000	200,000		
„ „ after treatment		9,000		150,000		
11. Number organisms added	20,500	30,000	15,250	32,500	5,000	10,000
„ „ after treatment		25,000		26,500		8,000
12. Number organisms added	250,000	15,000	25,000	2,500	2,500	2,500
„ „ after treatment		12,500		2,000		2,000
13. Number organisms added	100,000	250,000	250,000	35,000		
„ „ after treatment		250,000		30,000		
14. Number organisms added	1,500	95,000	40,000	5,250	5,000	20,000
„ „ after treatment		80,000		4,500		15,250
15. Number organisms added	50,250	32,500	6,500	96,800	30,000	25,000
„ „ after treatment		28,000		90,000		20,000

Soil, which had been sterilised in the autoclave under 15 lbs. pressure for half-an-hour, was inoculated with a counted suspension of trophic and cystic protozoa. It was then treated with 2 per cent. HCl. overnight, and the numbers counted by the dilution method. Fifteen such experiments were performed, given in Table II. On five other occasions two samples have been taken near to each other from the same field, and the number of protozoa in each sample found independently by two observers. The results so obtained were in every case identical.

Uneven distribution over the field. This possible source of error appears to us to have been obviated by the method of sampling we adopted. Reference to the map on p. 13 will show that if uneven distribution over the field is to account for the periodicity one must assume that active and cystic flagellates occupy alternate situations over the 14 rows which we sampled. Surely an impossible assumption!

The following experiments, however, will afford proof that the protozoa are fairly evenly distributed. In 1916–17 one of us took soil samples indiscriminately over the plot. These samples were counted and the results are given below.

	Sample	Amoebae	Flagellates
Feb. 16, 1916	1	2,500	50,000
	2	2,500	50,000
	3	2,500	50,000
May 30, 1917	1	3,750	17,500
	2	3,750	17,500
	3	3,750	17,500
	4	3,750	17,500

On March 9th, 1920 (two days after the daily sampling had ceased) two further samples were taken, B and C, and counted independently. The numbers were as follows:

	Total		Active		Cystic	
	Flagellates	Amoebae	Flagellates	Amoebae	Flagellates	Amoebae
Series B ...	9,000	2,500	6,500	2,150	2,500	350
„ C ...	9,000	3,250	5,750	2,650	3,250	600

These figures justify the belief that unequal distribution in the field cannot account for the flagellate periodicity.

Death of cysts due to action of 2 per cent. HCl. In the previous publications referred to above(5, 6) it was shown that a small proportion of the cysts might be killed by the acid; the proportion, however, was on the average below 15 per cent., which could not account for the marked differences obtained in the present series of experiments.

In each case the residual acid was determined by titration and found to be approximately constant, and as there had been so little variation in the conditions of working there is no reason to expect any variation in the action on the cysts. Samples 2, 5, 12, 18, 22 in Table I furnish examples. Here the total number of flagellates are nearly identical: the titration values for the samples are the same, but the number of active flagellates are very different. This also occurs with samples 13, 15, 16, 17.

DISCUSSION.

Table I and Fig. 3 clearly demonstrate a daily periodicity in the numbers of active forms of the three species of flagellates counted in our experiments. The rhythm is not obviously dependent on temperature or rainfall; for the curves of Fig. 7 show no relationship to the number of flagellates. Nor can we find evidence that any other external factor is the cause.

Preliminary experiments in laboratory cultures of the organisms maintained at a constant temperature of 20° C. indicate a similar periodicity. Further work on the subject is now in hand, and any detailed discussion of the causes of these daily fluctuations would be premature until more exact knowledge is gained of the life histories of the flagellates and the time required for the completion of each phase. Further, two of the flagellates—*Oicomonas* and *Cercomonas*—have two methods of reproduction—an asexual one by binary fission and a sexual one, where conjugation leads to cyst production (11), but little is known of the relationship between these two types of reproduction and the period of time occupied by each.

It seems safe to suppose, however, that the periodicity is a reproductive phenomenon. All through the animal kingdom, from the highest to the lowest class, breeding is a periodic phase, not only of the individual, but also of the species. In the protozoa the malaria parasite affords a good example. As is well known the attacks of fever coincide with the breaking up of the rosette phase of the parasite into merozites. Hence in the tertian ague, caused by *Plasmodium vivax*, fever returns every third day, and in quartian ague of *P. malariae*, every fourth day. Thus in these two species of Plasmodium there is a reproductive periodicity which may be kept up for months. A reproductive rhythm has been suggested in other species of protozoa by Calkins (3) for the fission rate of Paramecium, Woodruff (12) and Gregory (8) for this, and other ciliates, and by Boeck (1) for the encystment of Giardia. In the other phyla of the invertebrate kingdom periodicity obtains as in the egg-laying of *Convoluta*

described by Keeble (9). There is also the remarkable case of the Atlantic Palolo worm (*Eunice fucata*), which comes out of its hole to liberate the genital segments before dawn on the last quarter of the moon between June 20th and July 25th. H. G. Mayer states that neither the light nor the tide of the last quarter are necessary.

Further, Bohn in 1904 (2) records that sea shore snails taken far from the natural habitat maintain a rhythm synchronous with the tides for a considerable period.

Each group of the vertebrate kingdom affords examples of the same phenomenon, of which advantage is taken by breeders of mammals; for throughout the whole groups not only the individual, but also the species come "on heat" at periods very nearly identical. That this may be caused by external conditions is probable in certain classes, such as the *Amphibia* and *Reptilia*, but in the majority of cases such a connection has not been shown and "internal changes of the organisms" are now generally assumed. An excellent discussion of these phenomena is given in Marshall's book *The physiology of reproduction*.

Periodicity occurs so widely in all living things that by many people it is regarded as one of the characteristics of living matter. McClendon (10) in discussing the chemistry of vital phenomena says "One striking characteristic of the behaviour of organisms and parts of organisms is their periodicity. The human body shows a periodicity that is perhaps most strikingly demonstrated in fluctuations in temperature, being coldest some time near 3 a.m. and warmest about 10 a.m. Each organ has its characteristic periodicity—respiratory centre 16 and heart 72 per minute, and the motor ganglia 50 per second....This rhythm must be due therefore to metabolic changes."

These few examples are sufficient to demonstrate that the periodicity of soil flagellates though so striking, should not be regarded with surprise, but rather as a further example of a wide biological principle.

Numbers of Active Protozoa in relation to Bacterial Numbers.

We have reserved to the last the question of the relationship between bacterial numbers and those of active protozoa. Reference to Figs. 1, 3, 5 show that it is impossible to establish any correlation between the bacteria and the number of active flagellates; for while these vary rhythmically from day to day the bacteria show no such orderly fluctuations.

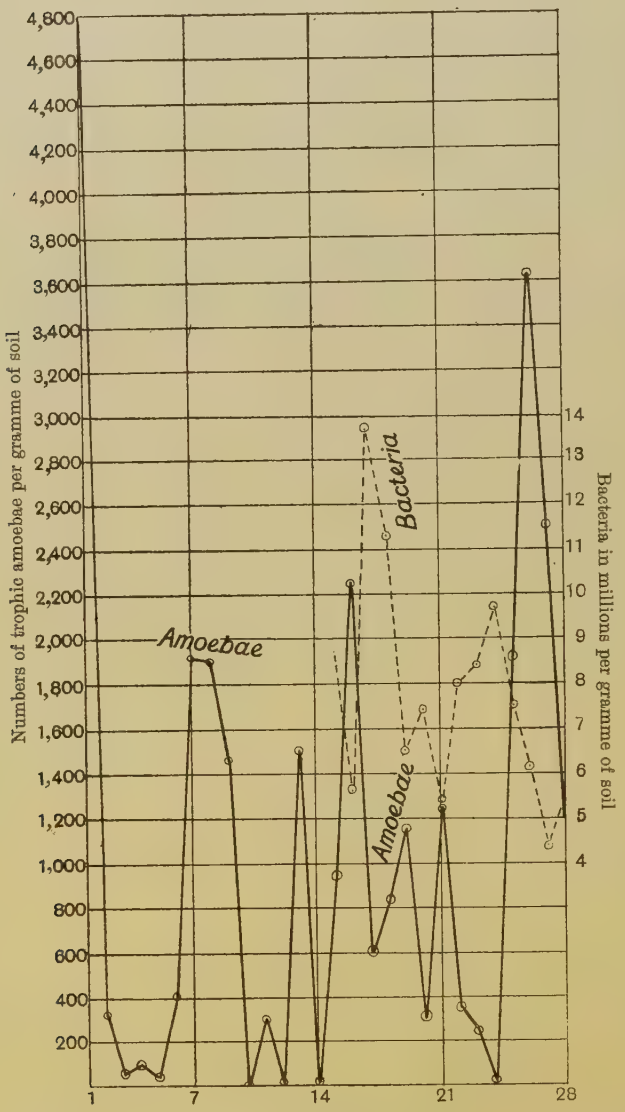


Fig. 5. Numbers of bacteria and trophic amoebae in Broadbalk, plot 2, from February 9—March 8, 1920. Daily countings.

Table III gives the number of bacteria per gr. of soil for 14 daily samples.

Table III.

Sample	Bacteria in millions per gr.	Sample	Bacteria in millions per gr.
15	8·75	22	8·0
16	5·575	23	8·375
17	13·75	24	9·75
18	11·325	25	7·5
19	6·5	26	6·15
20	7·4	27	4·425
21	5·4	28	5·4

The case is different, however, when the trophic amoebae are considered, the numbers of which are given in Table IV. Fig. 5 shows the bacterial and amoebic numbers in 14 daily samples. It is at once evident that there is a very close correlation between the two: without exception when the bacterial numbers are high those of the amoebae are low, and *vice versa*. Russell and Hutchinson postulated such a relationship in their partial sterilisation hypothesis, but we believe this is the first time it has been so clearly demonstrated[1]. By inoculating soil with *Amoeba limax* Goodey (7) was able to bring about a depression in bacterial numbers; but as far as we know data for a curve from ordinary field soil such as Fig. 5 has never before been obtained. This is primarily due to lack of methods. The earlier workers counted the total numbers of amoebae (trophic and cystic); this as was to be expected, gave variable results, and the method ought to be abandoned in future investigations. The second source of error was the length of time between the taking of the samples: they should be taken at frequent intervals, daily if possible. For example, examination of Fig. 5 shows that if after taking sample 17 an interval of three days had elapsed before another was taken both the bacterial and the amoebic numbers would have gone down, and a false conception of the relationship of the two would have resulted. A similar error would have resulted had no counts been taken between samples 19 and 25.

Table IV gives the total, active and cystic numbers per gr. of soil for the amoebae.

Fig. 1 appears to negative the contention of the necessity of daily sampling, for, with one exception the bacterial and amoebic curves fit

[1] Previous work by one of us showed that the experimental error by our mode of counting bacteria was 17 per cent. This, in the present experiments, would not vitiate the conclusion that there is interaction between amoebae and bacteria.

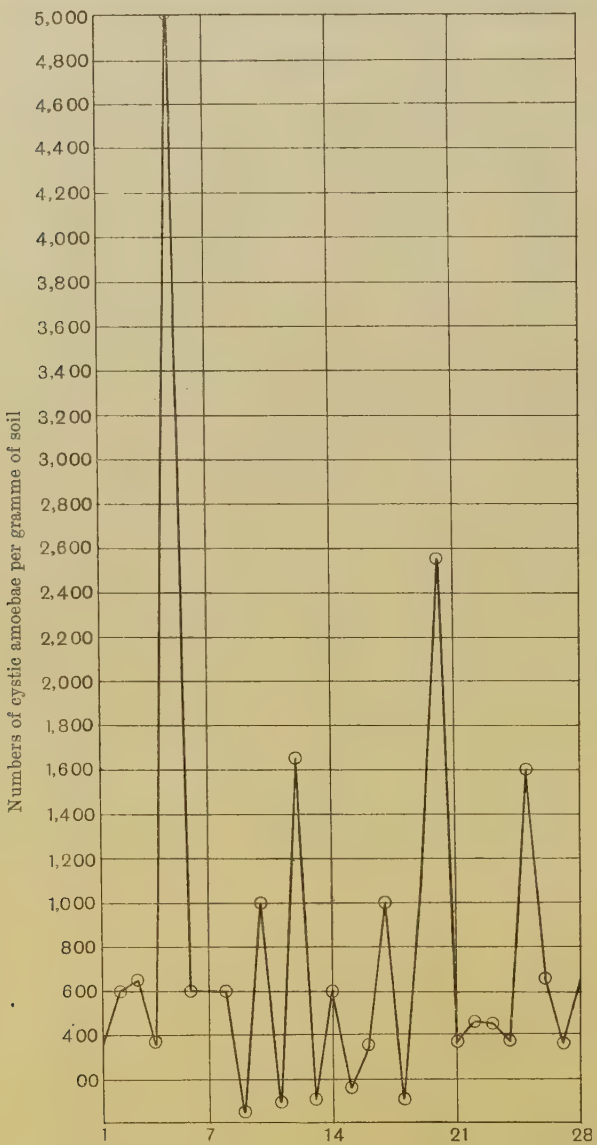


Fig. 6. Cystic amoebae in Broadbalk, plot 2, from February 9—March 8, 1920. Daily countings.

together quite well. This would often occur, but in many cases the correlation will break down if the intervals are long between the successive counts. Doubtless many of the numerous contradictory results in the earlier literature can be ascribed to this cause.

Table IV.

Sample	Total	Cystic	Active	Sample	Total	Cystic	Active
1	5,150	360	4,790	15	1,105	160	945
2	950	610	340	16	2,605	350	2,255
3	705	650	55	17	1,605	1,005	600
4	445	360	95	18	950	110	840
5	5,075	5,030	45	19	2,250	1,100	1,150
6	1,015	610	405	20	2,850	2,550	300
7	2,520	600	1,920	21	1,600	360	1,240
8	2,515	605	1,910	22	810	460	350
9	1,515	55	1,460	23	705	450	255
10	1,010	1,010	0	24	400	375	25
11	400	100	300	25	3,510	1,600	1,910
12	1,660	1,655	5	26	4,275	650	3,625
13	1,610	110	1,500	27	2,855	360	2,495
14	610	600	10	28	1,850	650	1,200

It would be premature to discuss the relation between the numbers of active and cystic amoebae, or the reason why, after a period of depression, the total number of amoebae should suddenly greatly increase.

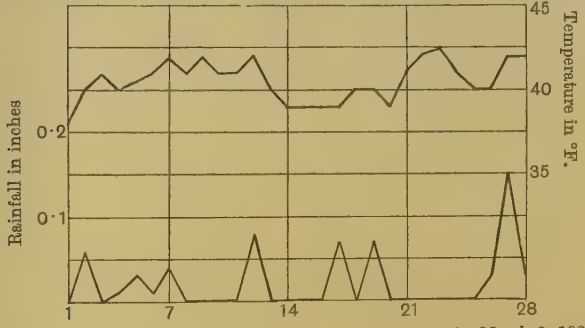


Fig. 7. Rainfall and ground temperature from February 9—March 8, 1920.

The answers to such questions are to be found in a knowledge of the life histories and physiology of these protozoa, which at present we do not possess.

It is hoped to continue the daily counts for a year to obtain data, which, with those yielded by pure culture study, may throw light on the principles underlying the daily fluctuations.

SUMMARY.

1. There is a daily fluctuation in the number of trophic forms of the three species of flagellates *Oicomonas* sp. (Martin), *Cercomonas longicauda* and Bodo sp., in the soil of arable fields.

2. The numbers of bacteria and trophic amoebae in the soil are correlated, varying inversely over a period of 14 days.

3. Temperature and rainfall appear to have no influence on the numbers of active protozoa in the soil.

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SPARTINA PROBLEMS.

By Prof. F. W. OLIVER, F.R.S.

(With 1 Plate and 3 text-figs.)

From time to time the attention, not merely of botanists, but of whole communities is rivetted by the sudden appearance of some unfamiliar plant which spreads everywhere in pure stands, often over great areas and to the almost entire exclusion of other forms of vegetation.

Familiar is the appearance of the fire weed or willow herb (*Epilobium angustifolium*) where forests have been burnt, charlock and field poppy where ground has been broken by the plough or, as in the devastated areas of France, by high explosive shells[1]. In such cases the character of the ground has been modified so as to favour the production of a new type of vegetation, a vegetation which springs suddenly perhaps from dormant seeds long present in the soil.

In other cases a like result is produced by the arrival and spread of some exotic plant gifted with great powers of dispersal such as the Russian thistle (*Salsola kali*) in N. America, and the prickly or pest pear (*Opuntia inermis*) in Queensland and New South Wales[2].

Where fresh water is at once the agent of dispersal and the medium in which the plant grows, very striking effects are apt to be produced—illustrated in recent years by the spread of the water hyacinth (*Eichhornia crassipes*) in the navigable waters of N. America (Florida) and Australia[3], and of Azolla in drains, lagoons and ponds in England and France. More than two generations ago (1842) the newly introduced Canadian waterweed (*Elodea canadensis*) spread with astonishing rapidity through the river and canal systems of England to the material hindrance of navigation and drainage. In this case propagation was certainly vegetative as Elodea is dioecious and female plants alone have been met with in this country. From Britain, Elodea made its way to the

[1] A. W. Hill, *Kew Bull. Misc. Inf.*, 1917, p. 297.

[2] The Prickly Pear in Australia, Com. of Australia, Inst. of Science and Industry, *Bull.* No. 12, 1919.

[3] H. J. Webber, The Water Hyacinth, *U.S. Dept. of Agric.*, Division of Botany, *Bull.* No. 18, 1897. Water Hyacinth in New South Wales, *Agr. Gaz. of N.S.W.*, Dec. 1906.

Continent where it spread for decades in ever widening circles till it lost itself in the waterless barriers of the Middle East.

The subject of the present article is *Spartina Townsendii*, a reed-like grass which is rapidly monopolising the extensive tidal mud flats of the south coast of England from Dorset to Sussex, with headquarters at Southampton and Poole Harbour. In addition to being a botanical phenomenon of the first order, perhaps unique in the recorded history of vegetation, the spread of Spartina is raising economic problems which will have to be grappled with sooner or later. Though still in the phase of youth Spartina already occupies dozens of square miles of mud flats in pure stands which continually get denser and denser. There seems little risk of error in asserting that in the future this area will expand to hundreds or thousands of miles. Subject to climatic limitations, wherever there is mud there will be Spartina. It is time for us to learn something about the properties of this amazing plant.

A century ago the only species of Spartina known in Europe was *S. stricta*, a low-growing species common on mud flats from Devon to Lincoln and on the Continent. In 1829 this was joined by a second species, *S. alterniflora*, supposed to have been introduced accidentally by shipping from America. Its occurrence in Southampton Water and at one other spot, the mouth of the River Adour, at the southern end of the Bay of Biscay, was well known to botanical geographers in the middle of last century[1]. In 1870 a third species, *S. Townsendii*, the subject of this article, made its appearance in Southampton Water, and it is the spread of this form in recent years which has attracted general attention. Gradually it has made its way east and west from Southampton along the sheltered coast line behind the Isle of Wight. It occurs in special abundance at the Beaulieu and Lymington Rivers and off Keyhaven, behind the Hurst Castle spit. In 1899 the first specimen was discovered in Poole Harbour[2] and in 20 years it has spread into all the inlets and bays in the most remarkable manner[3]. From Poole Harbour no specimens of either *S. stricta* or *S. alterniflora* have been reported.

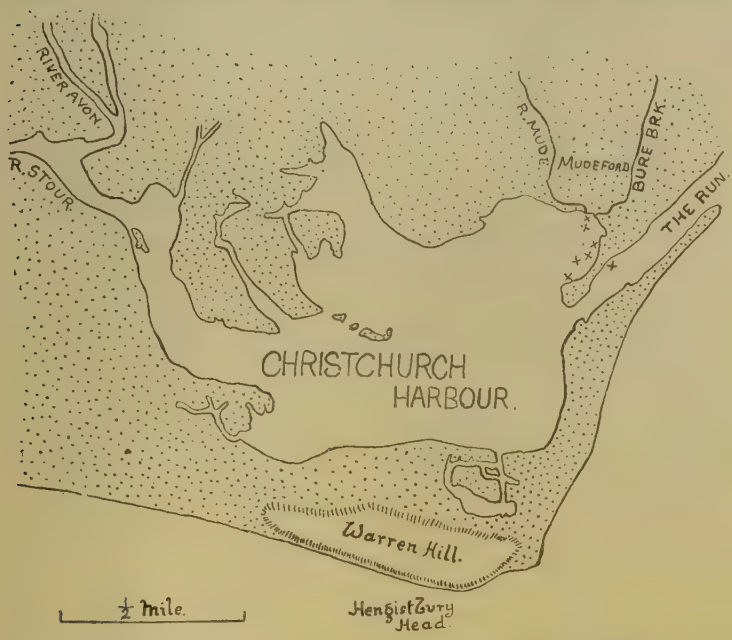
Into Christchurch Harbour, midway between Poole and Hurst Castle,

[1] A. De Candolle, *Géographie Botanique*, 1855, p. 1053.

[2] E. F. Linton, *Flora of Bournemouth*, p. 246.

[3] For a summary of records of the distribution of *Spartina Townsendii* and its allies, see O. Stapf: Mud-binding Grasses, *Kew Bull.*, 1907, p. 190; Gardener's *Chronicle*, *Spartina Townsendii*, 1908, p. 33; Townsend's Grass or Rice Grass, *Proc. Bournemouth Nat. Sci. Soc.*, Vol. v, 1913. For Poole Harbour, see R. V. Sherring's three Spartina Reports in *Proc. Bournemouth Nat. Sci. Soc.*, Vols. v, vii and ix.

it penetrated in 1913 and has now established itself in sufficient strength to continue the invasion in force[1]. To the East, whilst Portsmouth,



Text-fig. 1. Sketch map of Christchurch Harbour (Hants.) showing the distribution of *Spartina Townsendii*, Nov. 1919. The clumps are marked by crosses, × ×. The first plant to settle was the one in The Run (1913); it is now 6 ft. across and is seen in the foreground of Pl. II, fig. 1. Land surfaces not covered by ordinary high tides are dotted. Charted by the Rev. C. O. S. Hatton.

[1] The following notes, from the Rev. C. O. S. Hatton, of Hinton Vicarage, Christchurch, who has kept in touch with this invasion from the first, are of unusual interest. I am much indebted to his courtesy in letting me publish them here.

"The first plant I noticed (and I feel pretty sure it was the first in the harbour) was in a little bit of backwater off the channel which connects the harbour and the sea. It was not at all a good position for it, being constantly covered with dead seaweed, etc. There were only a few blades when I first saw it in 1913, and it did not flower till 1917 when it produced two spikes. Having by that time grown high enough not to be constantly covered with rubbish it grew more quickly, and in 1918 there were about two dozen flower spikes and this year [1919] it flowered well and is now a circular clump about 2 yards across (cf. Fig. 1, Pl. II). I noticed one or two other clumps in the harbour in 1918 and this year [1919] I counted five others, growing well, also a good deal growing amongst other vegetation on the E. side of the harbour. The part where the new patches have sprung up is an ideal situation and I have no doubt that in a few years it will cover many acres of the present harbour. I should say that Christchurch Harbour is even more suitable for the Spartina than Poole and I shall be surprised if it does not spread even faster there."

Langston and Chichester Harbours have been long in occupation, Spartina has at length rounded Selsey Bill and got a footing in Pagham Harbour—though as recently as 1917 none was reported by botanists searching these muds. Apart from introductions for experimental pur-

Text-fig. 2. Sketch map of Pagham Harbour (Sussex) showing the distribution of *Spartina Townsendii*, Nov. 1919. The clumps are marked by crosses × ×, and are mostly about 2 ft. in diameter. Land above tidal range dotted. Charted by Dr and Miss Barford.

poses, referred to at p. 35, the above cover all known British localities to which the plant has spread by natural agencies. Some ten years ago it was reported as having reached the French coast (Rivers Saire and Vire in the Cherbourg peninsula) but no further information as to its spread in France is available[1].

[1] O. Stapf, *Townsend's Grass or Rice Grass*, p. 5 of reprint.

THE ORIGIN OF *SPARTINA TOWNSENDII*.

This species of Spartina is unknown anywhere in the world except at Southampton, where it originated, and in the adjacent waters which it has since invaded. There is no reason therefore for regarding it, like *S. alterniflora*, as an introduced plant. On the contrary, it must have been produced *in situ*. The current hypothesis, though not yet scientifically grounded, is that *S. Townsendii* is a naturally produced hybrid between *S. stricta* and *S. alterniflora*. This view we owe to Dr O. Stapf who has also made available a great deal of botanical information bearing on the plant.

This hypothesis is strengthened by the fact that at the mouth of the River Adour, near Bayonne, where, as at Southampton, *S. stricta* and *alterniflora* also occurred side by side, a new form named *S. Neyrautii*, having much in common with *S. Townsendii*, has appeared. The presumption is of course that both forms are spontaneous hybrids which have appeared at the only spots where such a thing was possible, i.e. at the only known spots where the two parent forms occurred together.

In support of the hybrid nature of *S. Townsendii* the extraordinary vigour of its growth and spread may be cited. In this connection attention has recently been drawn by Dr Augustine Henry to the hybrid nature of not a few forest trees of great vigour of growth and large output of timber. Dr Henry was so much impressed by the matter that he has engaged in the experimental production of hybrid trees with a view to providing forms suitable for use in afforesting the British Isles[1].

On the other hand if *Spartina Townsendii* is really a first cross and if, as seems almost certain, it is largely propagated and spread by seed, it is surprising that there is no evidence of segregation, i.e. of separation into the parent forms.

This anomaly needs clearing up, and, now that it is of general interest, it is much to be hoped some competent plant breeder may be disposed to take up the matter experimentally.

OCCURRENCE AND ECOLOGY.

The ground on which Spartina thrives best is the soft mud flats within 3 ft. of high water mark, such as are characteristic of Poole Harbour and Southampton. Prior to its appearance these flats were extensively occupied by the sea grass (*Zostera*), the ribbon-like leaves of which lie prone on the mud. With the advent of Spartina as the tufts

[1] A. Henry, The Artificial Production of vigorous trees, *Journ. Dept. Agr.*, Ireland, Oct., 1914.

close together Zostera is annihilated, the principal representative of the associated ground vegetation being a small form of the alga Enteromorpha. The higher levels of the flats are the first to be colonised. At first single isolated plants appear, presumed to be seedlings; each plant spreads laterally by means of stolons to form a circular or oval patch; the rate of growth in any direction being from 2–3 ft. per annum under favourable conditions. In this way the expanding tufts soon unite into strips with open passages between—like a jigsaw puzzle approaching completion—and finally meadow into practically continuous stretches covering acres of mud (cf. Pl. II, fig. 2).

In their earlier stages the height of the grass shoots is uniform over the patches, but as they expand (e.g. at 5–6 ft. diameter) the patches become saucer-shaped owing to the haulms of the central, older parts falling short of those at the periphery[1]. With the further extension of the patches this marginal effect, though still persisting, becomes less noticeable.

The height reached by the grass in its growth varies from season to season, depending particularly on the rainfall in the earlier part of the summer. In this respect Spartina resembles Salicornia and the other halophytes of the salt marsh. Flowering is spread over a long period (July–November) with maximum in September. It is stated to be a shy seeder in most seasons, with occasional bumper years.

Spartina roots very freely from its underground stems. There are two types of root: (1) long, anchoring roots which descend unbranched in the mud for 2 or even 3 ft.; (2) short, branched, superficial feeding roots, so closely crowded together as to form a continuous plexus in the surface layer (cf. Fig. 3; the sketch is reduced to $\frac{1}{3}$ nat. size).

A marked effect of Spartina is the collection and holding of suspended mud. The rise in level from this cause will sometimes reach as much as 4 or 5 inches in a year, though it is not implied that this rate of accretion is maintained indefinitely. The presence of the plant has a marked stabilising effect on the mud, so much so that it is possible to walk about on the meadows in relative safety.

Except where the Spartina meadows approach the shore they form pure stands, free from invasion by other halophytes. It seems too early to say whether Spartina is destined ultimately to give place to other vegetation, though judging from analogous cases such replacement may be regarded as probable. Should such a succession occur there is no

[1] At the present time this "marginal effect" is well shown by numerous patches of Spartina in Holes Bay bordering the L.& S.W. Railway to the west of Poole Station.

Text-fig. 3. Young ? seedling plant of *Spartina Townsendii*, not yet in the flowering stage (Nov. 1916). At the base, several stolons emerging from dense felt of surface roots; lower down are the long anchoring roots which may reach a depth of 2–3 feet.

reason to suppose that the saltings built up by Spartina would degenerate or yield up the mud which had been accreted. The Spartina would have done its work.

During the summer of 1919 a certain number of Spartina plants have been washed out of the mud of Poole Harbour and drifted down to the mouth. As these plants are quite intact they can only have been loosened by lateral erosion—due probably to some migrating creek undercutting one of the meadows. This is an ordinary occurrence on every salt marsh and cannot be made the ground for supposing that any general disappearance of Spartina is foreshadowed.

Near the shore line Spartina often comes into relation with *Scirpus maritimus*, *Juncus maritimus* and *J. Gerardi*, the meadows closing in and cutting off the free connection of these plants with open waters. Cases have been observed (e.g. to the west of Fitzworth Point, Poole Harbour) where Scirpus thus surrounded is dying wholesale—a result which may be due to competition, though it is premature to dogmatise. On the other hand where Spartina meets *Juncus Gerardi* (as at the head of Brands Bay, Poole Harbour) the latter, to judge from appearances, seems quite capable of holding its own.

From this slight sketch of the ecology of Spartina it is evident much remains to be done in the way of field observations of all sorts. Not only are the details of the life history largely unknown—it is doubtful if the history of a single plant of Spartina has been traced from the seedling or gemmule stage to the established clump. The relative importance played in distribution by seed and detached vegetative fragments has still to be ascertained.

It is evident that intensive work of this kind can only be done locally by persons on the spot. From the special nature of the habitat Spartina studies are an acquired taste. Every visit to a clump requires the use of mud boards on the feet, whilst the occurrence in these waters of four tides a day circumscribes opportunity of access.

Great value attaches to the systematic records of the spread of Spartina in Poole Harbour which Mr R. V. Sherring has undertaken. It is much to be hoped that his copious notes and photographic survey of the yearly advance may be published in collected form.

ECONOMIC ASPECTS.

The appearance on our shores of a new and vigorous plant like Spartina with its great capacity for accreting mud and its promise of indefinite spread raise the vital question of its probable effect on navi-

gation in the waters concerned; in addition there are several economic applications to which Spartina may lend itself.

1. Navigation.

Though other navigable waters will doubtless be involved it is convenient to restrict the present discussion to the case of Poole Harbour, where Spartina has been steadily spreading for 20 years.

After the object lesson of the great war no one is likely to question the assertion that it is a national interest that Poole Harbour should remain a place primarily for ships and fishermen. And yet the idea of extensive reclamation is hard to resist in view of the great Spartina meadows which are everywhere appearing. As a Poole fisherman put it, after helping to harvest a sample of the grass for a paper making trial, "You'll see, me and my brother will be farmers yet."

The danger to navigation inherent in reclamation is this. When parts of a tidal estuary are banked off and removed from tidal action, by so much is storage space for water diminished; and this amount will be lacking for scour at the ebb. The result is that the channels become choked and navigation suffers.

Suppose for example five square miles of the estuary carrying on the average a depth of 2 ft. of water at the spring tides to be banked off. This would mean a deficit of about 280 million cubic feet—a volume of water far from negligible in this connection. The history of not a few decayed ports shows that there exists eternal antagonism between agriculture and navigation. When prices of produce rule high the land tends to encroach on the waters. The immediate gain is obvious and tangible, the ultimate consequences remote and shadowy. Amid a multiplicity of authorities the frontagers are apt to help themselves unless the community is unusually vigilant.

No one can foretell with absolute certainty what will happen as a consequence of the spread of Spartina. There is an unknown factor, the persistence of this new invader. At the same time there are no signs of respite and it will be safest to assume the worst.

The action of Spartina may be pictured as follows. The plant spreads rapidly on the mud flats and tends to fix such mobile mud as may be drifted over it. In this way in proportion as the flats are colonised by Spartina their level rises.

The immediate source of the mud which Spartina is fixing will be the sides and bottoms of the channels, though a certain very small amount of this will be made good by new mud entering the harbour by

the rivers which discharge into it. In its present phase Spartina has an insatiable appetite for mud with the result that much mud is being transferred from lower to higher levels. As the new mud entering is almost negligible in amount what is taking place is substantially of the nature of a redistribution of mud already present.

Corresponding to this phase a widening and deepening of the channels is to be expected, an assumption which appears to agree with local observation.

As time goes on and the Spartina spread approaches its limits the rate of assimilation of mud in the higher levels will be abated. The early hunger for mud having been satisfied the final rise in level (as the height of the flats approaches the limits of tidal rise) will be much more gradual than in the preceding phase.

Following such a redistribution of mud, two consequences are to be expected. (1) Owing to the increased sectional areas of the channels the rate of flow would be slowed and (2) the tidal water, being largely displaced by mud in the higher levels, would occupy on the average a lower level than was the case before the advent of Spartina.

Both these effects, i.e. the slowing of the currents and the lesser head of tidal water should work towards a diminution of scouring power at the ebb. The mouth would thus tend to become encumbered with silt to the impairment of navigation.

But Poole Harbour is singular in its construction from the extreme narrowness of its mouth. The area of the harbour is roughly 20 square miles, whilst the outlet is only 350 yards wide. As a consequence the harbour is stated never really to fill at high tide, i.e. to reach the full height to which it is potentially entitled, because the tidal wave outside passes the mouth too quickly.

Based on the existence of a substantial difference in level between high tide within and high tide without, the theory obtains locally that, after all, Poole Harbour may prove immune to the usual consequences of excessive silting. As the Spartina completes its work and the mud is transferred from the bottom to the top, the tide will have less far to go and will no longer waste the precious moments in excessive lateral travel. On the contrary it is expected by local optimists that in fulness of time the tide will rise in the channels to an appreciably higher level than it does at present. Hence it seems to follow that, taken in connection with the unexhausted head of water outside, Spartina is to be hailed as the regenerator and not as the probable destroyer of the régime of Poole Harbour. In other words the one thing required to remove the defect

of a harbour too big for its mouth was the arrival of just such a vigorous agent of reclamation as Spartina is proving itself to be!

The dissemination of this theory in its unproved state is dangerous if not vicious. It is one of those comforting theories which beguiles human nature into sitting tight and doing nothing. It is much more agreeable to "wait and see" than to take the arduous but necessary steps towards finding out. Spartina has now been encroaching for 20 years and systematic observations should reveal whether the trend of change is in the direction implied by this theory. Meanwhile, what is the experience with other narrow mouthed harbours? Are they immune from deterioration when halophytic vegetation invades their mud flats?

2. Spartina as an Agent in Reclamation.

It is obvious that a vigorous plant like Spartina, capable of colonising soft and mobile mud flats, must have considerable value from this point of view. In Britain roots have been transplanted to a number of localities with a view to studying the behaviour of Spartina under varying surroundings. Among these may be mentioned the Firth of Forth, Wells (Norfolk), and the Harwich estuary. At Clevedon (Somerset)[1] and Sheerness it has been planted with the definite object of protecting the coast line from erosion by scour, and with considerable success, so it appears. Further afield consignments have been sent to New Zealand, Australia, S. America and other distant spots, and when the time is ready it is much to be hoped that a collective report may be prepared detailing the results of all such experiments. The notice which Spartina as a reclaiming agent has received from overseas is noteworthy and the demand appears to be increasing. It will perhaps be convenient to state here that Lord Montagu of Beaulieu is always willing to deal with applications of this kind.

3. As a Feed for Stock.

No one who has lived on a farm, bordering e.g. on Poole Harbour, can have remained in doubt as to the value of Spartina in the feeding of stock. Horses, sheep and cattle eat it with avidity and habitually make their way on to the Spartina meadows almost before the tide has run off. Farmers speak well of it except that it gives an undesirable flavour to milk. As the grass remains standing on its roots throughout the winter till April, it forms a most convenient reserve feed that can be cut as required.

[1] According to information from Miss I. M. Roper.

So far as we know analyses have not been published, nor proper feeding trials conducted. It is desirable that both these matters should be put through and the results made known. On the coast of New England related species of Spartina are regularly harvested and the hay fed to cattle[1].

4. As a Raw Material for Paper.

The presence of a tall growing grass like Spartina in pure stands of almost unlimited extent suggested the possibility of its employment as a paper-making material. A preliminary sample was submitted to the late Mr Clayton Beadle, the well-known paper expert, in July 1916, and as a result of his encouraging report steps were taken to collect larger samples for trial at a paper mill.

With the approval and assistance of the Poole Harbour Board large cuts of Spartina were made in October 1916 and in March 1917. These were forwarded to Messrs Thomas and Green, Paper Makers, who converted them into paper at their mills at Wooburn in Bucks.

The October cut was sent green and wet and after washing at the mills, was boiled wet.

The March sample was dried as well as the conditions at the time allowed and was boiled dry.

Both samples contained a good deal of mud which could not be altogether removed by mechanical means and persisted as black specks in the paper.

By the summer of 1917 labour being unobtainable at Poole, a squad of boys and girls from Oldfeld School, Swanage, was organised by Mr B. K. Hunter for an August Spartina camp at Ower on the Studland side of Poole Harbour. This camp was repeated in August 1918.

The work of these camps consisted in mowing and bringing the grass ashore, washing it and picking out the dead stalks of previous seasons, transporting it to the drying ground where it was spread out in the sun, and when dry sacking it and getting it on to the rail.

As these two cuts from the Ower camp do not together make an economic sample for boiling (about 4 tons dry weight) they are being kept in store till the balance can be sent. In 1919 it was not possible to hold a Spartina camp but it is hoped in 1920 that the job may be completed.

[1] F. Lamson-Scribner, Grasses of Salt Marshes, *Yearbook U.S. Dept. of Agric.* 1895, p. 324.

In spite of this postponement, several additional small samples have been treated, and a great deal of experience gained in methods of harvesting, etc.

The notes which follow are provisional conclusions based on the experience of 1916 to 1918.

(1) *Harvesting.* The proper time to cut the grass is in August when it has reached its full growth, and whilst there still remains probability of several weeks drying weather. It is best cut with a scythe a day or two before the spring tides. The grass should be left in swaythes just as it falls and not carried ashore. The spring tides will float it, and if the area cut be surrounded by corked ropes or spars lashed together the cut will not drift beyond this enclosure which can be towed to some convenient spot at high water.

The grass will be efficiently cleansed of mud by the scour of the tide as it runs through it so that special cleaning by hand is superfluous.

In the case of areas not previously cut many old haulms of previous years are mingled in the current growth. These have to be picked out by hand before the grass is spread out to dry, as old rotten fibre spoils the paper pulp. The labour involved in this operation is enormous. If one man can pick a stone of wet grass (i.e. separate the current growth from that of previous years) in an hour it will require 160 man hours to pick over a ton. In other words the picking over of this amount is a week's job for four men of the "casual" order. Trained labourers would of course work much more rapidly. This picking is the limiting factor in harvesting Spartina and accounts for the small output of our Spartina camps. One man can mow in two days more grass than 12 boys can pick over in a week.

However, should Spartina ever be regularly exploited the need for this operation of picking over will disappear. For when an area has been cut, next year's crop will be free from old stalks and can be harvested in its entirety. Small experimental areas have been cut for three successive years and we find no appreciable diminution of the yield: at any rate the fluctuations are within the range of purely seasonal factors. So that it comes to this. The cut after the first year can be taken entire and can be freed of mud by letting the tide scour it. No hand labour is required other than that involved in mowing and transporting the cut to the drying grounds. A good yield would be two tons (dry weight) per acre. Whether it may not be desirable to let an occasional year pass without cutting we are unable to say. There is always a danger

of overcropping, and if exploitation should be undertaken the matter will have to be carefully considered[1].

Our experience of drying is confined to natural means. Spread out on exposed wind-swept ground in fine weather (August and September) the cut should be dry in three weeks. If through broken weather it is still wet by the middle of September there may be difficulty in saving the crop. Drying is hastened by arranging the grass in little stooks or resting it against brushwood or hurdles. On the whole with vigilance and judicious handling the crop should be capable of natural-drying three years out of four. But the possibilities of artificial drying deserve serious consideration.

(2) *Conversion into pulp.* In the trials hitherto carried out the Spartina fibre has been boiled and bleached according to the standard treatment for esparto. Though the pulp possesses distinctly useful qualities in paper-making we prefer to speak here of some of its shortcomings, as the correction of these is a necessary preliminary to its adoption. Some of these are uncurable, such as the yield, which averages 30 per cent. on the dry weight of fibre boiled. This defect it is to be hoped may be compensated by the purity and density of the stands, the relative ease of harvesting and the proximity of the home market. Meanwhile there is the difficulty of bleaching the pulp to a satisfactory colour. Until this is solved by a special chemical research it is hopeless to think of Spartina as a material for fine papers. Should the bleaching problem prove insoluble *Spartina Townsendii* could probably be converted into straw boards as was the related American slough grass (*Spartina michauxiana*) at Quincy in Ohio.

Another trouble concerns the hydration of the pulp; Spartina-pulp is rather apt to "run wet" on the paper-making machine, a defect which may depend (as some experts suspect) on its marine origin—a new factor in the origin of these raw materials. These and other matters of like nature will have to be smoothed out before Spartina can take its place in the paper industry, just as must always have been the case with other raw materials in this and other industries. Whatever may come of the present project it is hard to believe that at some future time, when Spartina has spread into all the muds of our shores, this plant will not find a use in the paper-making world. Allowing for an average yield of two tons dry weight per acre enough Spartina is already present in these waters to feed a mill all the year round with 100 to 150 tons per week.

[1] The collection of esparto grass is carefully regulated in this sense. Cf. H. de Montessus de Ballore, *Alfa et papier d'alfa* (Dunod and Pinat, 1909), p. 9.

Fig. 1.

Fig. 2.

Fig. 3.

Other uses for Spartina are sure to present themselves as knowledge increases of the ways in which plants may be chemically exploited for particular purposes. The important points in the present case are the extent, purity and density of the stands, combined with relative ease of cutting and transport.

Really in Spartina we have a subject that seems to call for facilities for investigation such as can only be provided by what for want of a better name may be termed a Spartina Institute located on the spot.

From every point of view full knowledge is required, alike whether the plant be regarded as a botanical phenomenon, a weed which seriously threatens navigation, or a gift of providence capable of being put to a variety of uses.

DESCRIPTION OF PHOTOGRAPHS ON PLATE II

Fig. 1. The original clump of *Spartina Townsendii* which established itself in 1913 on the north side of the outlet of Christchurch Harbour. Longest diameter of clump 6 ft. Photo. taken Nov. 1919 and communicated by the Rev. C. O. S. Hatton.

Fig. 2. Spartina field in Brands Bay, Poole Harbour, showing a characteristic phase in colonisation. Taken from the south side of Goathorn Point looking S.W. E. J. Salisbury, photo. Aug. 1919.

Fig. 3. Clump of Spartina in flower. The white appendages are the stigmas. E. J. Salisbury, photo. Aug., 1919.

INVESTIGATION OF THE NATURE AND CAUSE OF THE DAMAGE TO PLANT TISSUE RESULTING FROM THE FEEDING OF CAPSID BUGS.

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(With 1 Plate and 5 text-figures.)

This piece of work was suggested by Mr J. C. F. Fryer, entomologist to the Ministry of Agriculture and was carried out at the Royal College of Science, S. Kensington, under Prof. H. Maxwell Lefroy.

I wish to acknowledge my indebtedness to Prof. Blackman and Dr S. G. Paine, of the Imperial College of Science and Technology, for much valuable assistance and advice.

The object of this investigation was to discover the causes of the damage to plants and especially to apple trees from the feeding of Capsid bugs. There are many species of Capsids which normally feed on the fruit and leaves of apple trees in this country, those which have attracted most attention being the following: *Plesiocoris rugicollis*, *Atractotomus mali*, *Orthotylus marginalis* and *Psallus ambiguus*; only the first-named causes any damage to the fruit and foliage (Fryer(1), Petherbridge and Husain(2) and others). *Lygus pratensis* also is found by Collinge(3), to cause damage to the apple fruit itself by depositing its eggs in the lenticels, but not by sucking the juices. The problem to be solved is, then, as follows. There are four species of Capsid bugs, mostly closely allied, all feeding on apple fruit and foliage and feeding by the same process, i.e. by inserting their mouth-parts into the tissue and sucking the sap, yet only one of them, *Plesiocoris rugicollis*, causes any damage.

P. rugicollis hatches out in May, and the young Capsids immediately begin to feed voraciously, picking out the young shoots which soon become covered with spots and patches of dead cells; this has the effect of keeping back the shoots and young leaves to a very large extent, and in some cases causes the death of the whole shoot. When the young

apples begin to form, the Capsids transfer their attention to these, which in their turn become rapidly covered with red spots, each spot, of course, marking the point of insertion of the stylets. Thus far the injury to the apple appears identical with that of the leaf, but after a short time the apple becomes cracked, a corky layer is formed, and a very distorted fruit results; in many cases the badly attacked apple ceases to grow and falls off. This is in marked contrast to the other three species mentioned above which feed in a similar manner and yet produce no ill effects whatever. The question then arises, what is there about this particular species in contrast with the others, that the sucking action should be followed by so lethal an effect upon the tissues of the foliage and fruit.

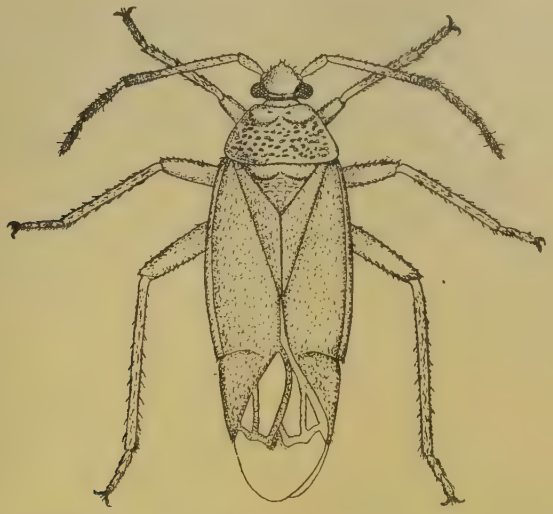

Fig. 1. Adult specimen of *Plesiocoris rugicollis*. After Petherbridge and Husain.

When this bug has sucked some of the sap, which it does by pushing its sharp stylets into the tissue and drawing up the liquid by means of a powerful pump situated in the head, at the same time injecting saliva into the wound (Awati(4)), the stylets are withdrawn and inserted elsewhere, meanwhile a drop of fluid gathers at the first puncture gradually getting larger as the cells are killed and yield up their contents. When this drop has dried up, the cells underlying it are all killed leaving a large discoloured patch which may continue to spread slightly especially if in the neighbourhood of a vein.

In the case of the apple fruit these dead cells present a dark red or brown appearance owing to the formation of a tannin which gives a black coloration with ferrous sulphate. Microtome sections of portions of apple leaf injured by *P. rugicollis* show a mass of dead cells filled with a red granular material, the epidermis dying after the mesophyll, this confirms Petherbridge and Husain (2). When *P. rugicollis* feeds on Willow a clear space is produced round each puncture so that if damaged by several punctures the leaf becomes transparent and dies. Sections of such a leaf show that the cells are killed and filled with a clear substance very similar in appearance to that found in the cells of the apple, so that the reaction appears identical with that produced in the apple, with the exception of the colour reaction. The production of the red-brown pigment is merely a death phenomenon of the apple cells and is no special reaction to the Capsid; apple leaves if held in chloroform vapour produce the same red pigment.

We come now to consider the possible explanations of this damage. These seem to be three:

Firstly, a purely mechanical injury caused by the laceration of the tissues by the stylets in process of sucking.

Secondly, the possibility of the bug acting as a "carrier" of bacteria and injecting them into the plant along with the salivary juices and so setting up a pathological state. An interesting parallel to this is found in the case of the Beet Leaf hopper which carries the germs of beet curly top (Stahl and Carsner (5)).

Thirdly, the injection of some secretion, either from the salivary glands, which is the more probable, or a regurgitation from the stomach which has a virulent toxic effect on the tissue. These three theories seem to cover the only possible explanations of the damage. As has been mentioned already, the formation of the red brown pigment is a death phenomenon of the apple and it is possible by means of laceration with a sterile needle to produce a small brown spot similar in appearance to that produced by the Capsid but not approaching it in extent of the injury. The following attempts were made with sterile needles of varying fineness to reproduce the injury caused by the bugs.

(1) Scratch on the surface of the leaf with a dry sterile needle.
(2) Puncture with dry sterile needle.
(3) Scratch through sterile water.
(4) Puncture through sterile water.
(5) Puncture with dry needle not penetrating the leaf.

In each case only cells actually lacerated by the needles were killed,

the injury did not spread and the leaves were not put back in their development.

If it is assumed that the injury is due to the mechanical laceration of the cells and their consequent loss of sap by the stylets of the bug, then the question arises, why do not the other species of apple feeding bugs produce the same effect? as the methods of feeding, and the mandibles and maxillary stylets are precisely the same in each case.

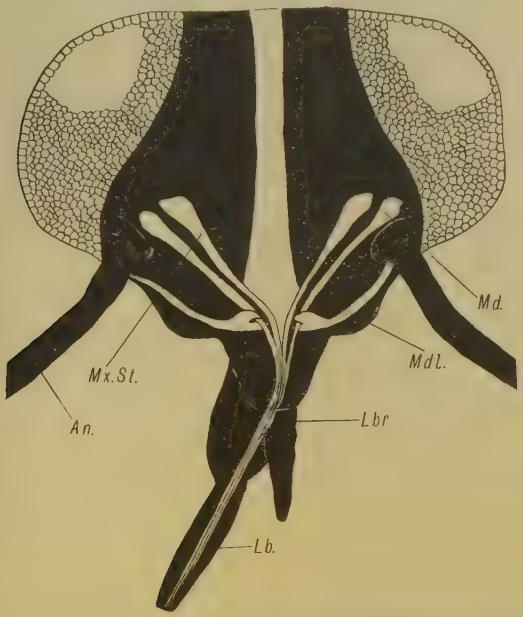

Fig. 2. Semi-diagrammatic drawing of the head of *Lygus pabulinus* showing mouth parts.

Attempts were made under the binocular microscope to pierce the leaf with the mouth-parts of various species after they had been removed from the head so that there was no possibility of any salivary juices being injected: this was not very satisfactory owing to the extreme fineness of the stylets, but in a few instances perforation was effected but with no visible results, the stylets apparently being too minute to kill more than one or two cells by laceration. As regards the possibility of the loss of sap by sucking causing the damage, if this were so it would of necessity follow that all the species of Capsids and indeed any sucking insect should produce similar harmful results.

Taking all these facts into consideration, it will be seen that mechanical injury alone is not sufficient to account for such serious damage.

Turning now to the second possible explanation, that of injection of bacteria with the salivary juices, the following experiments were made to decide this point:

Very thin microtome sections of the salivary glands of *Plesiocoris rugicollis* and one or two other apple feeding bugs were cut in order to verify if possible, the presence of bacteria in the glands and ducts; the sections were stained with various bacterial stains, such as Victoria Blue, Carbol Fuchsin, Gram's Stain etc., but in no case were there any indications of bacteria. Sections were also cut of the damaged portions of apple and willow leaves and stained with various bacterial stains as above, in order to trace bacteria in the cells. Although some of the cells presented a slightly granular appearance, this was found to be due to the presence of the tannin and no bacteria could be discovered. Apple leaves badly damaged by *P. rugicollis* were then taken and ground up with sterile sand in a mortar under sterile conditions with the addition of a little sterile water, the resulting extract was allowed to stand and the clear red fluid drawn off, it was then injected with a sterile hypodermic syringe into undamaged apple and willow leaves. A solution of damaged willow leaf was made under similar conditions and also injected into apple and willow leaves.

The inoculations made were as follows:

(1) Inoculation of apple leaf with sterile water control.

(2) Inoculation of apple leaf with extract of damaged apple leaf.

(3) Inoculation of apple leaf with extract as in (2) but boiled.

(4) Inoculation of apple leaf with a similar extract of willow leaves damaged by the same insect.

(5) Inoculation of apple leaf extract as in (4) but boiled.

A certain amount of damage was produced in each case, very slightly more marked in (2) and (4) than in the others. Five precisely similar injections were then made into willow leaves, these gave negative results, only such cells as actually came into contact with the hypodermic needle apparently being affected.

Bacterial cultures were then made from the damaged leaves as follows. The leaves were ground up as before with sterile sand and sterile water under sterile conditions and a drop of the resulting fluid was added to 10 c.c. of sterile water and plated out on various media, Turnip Agar + 4, Potato Mush Agar, Beef Agar, etc., after five days many small round colonies were observed, these were plated out until

a pure culture of a bright chrome-red organism was obtained. A number of the harmless apple-feeding Capsids in a starved condition were then introduced into a petri dish containing the above culture; after they had all been observed to insert their stylets into the medium and to be well plastered with the colonies, they were transferred to a fresh young apple shoot and allowed to feed, no damage resulted. Suspensions were then made of the colonies and injected by means of a sterile syringe as follows into both apple and willow leaves:

(1) Sterile water control.

(2) Suspension of living bacteria.

(3) Suspension of dead bacteria (boiled).

A larger area of damage was caused by (2) and (3) than by the control, there presumably being a toxin present due to the presence of the bacteria in the injection, but as the damage caused by (3) was

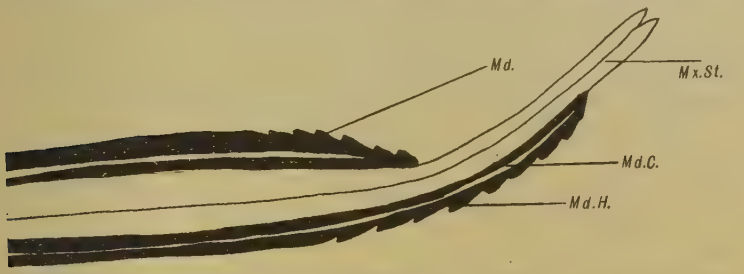

Fig. 3. Mandibles and maxillae of *Lygus pabulinus*. Drawn with the camera lucida, under the $\frac{1}{12}$ oil immersion, ocular 4.

precisely similar to that caused by (2), it cannot be taken as evidence that bacteria are the cause of the injury under investigation.

Inoculations were then made with a number of common bacterial saprophytes, including the red organism already mentioned, in order to find out if any of them would continue to live saprophytically in the plant tissue if entrance were made for them, either artificially by the needle or by the Capsid's stylets, and if so, whether they would produce damage similar to that known to follow the feeding of *P. rugicollis*.

The following inoculations were made into apple leaf:

(1) Suspensions of the red bacteria isolated from the damaged apple leaf.

(2) The same with dead bacteria.

(3) Suspension of *Bacillus mesentericus*.

(4) Suspension as in (3) but boiled.

(5) Suspension of *Bacillus vulgaris*.
(6) Suspension as in (5) but boiled.
(7) Suspension of *Bacillus subtilis*.
(8) Suspension as in (7) but boiled.
(9) Suspension of *Bacillus mycoides*.
(10) Suspension as in (9) but boiled.

These inoculations were also made into willow leaves. In each case only slight damage was caused, in no way comparable to that produced by the Capsid.

The foregoing experiments seem to prove conclusively that bacteria play no part in producing the damage resulting from the feeding of the bug. The fact that the insects from the moment of hatching produce the same damage as the adults, also militates very strongly against the theory of bacterial infection as it would necessitate the bacteria passing on from generation to generation and also their having to pass the winter in the egg. The chrome-red colonies of bacteria which were isolated from the damaged apple leaf were presumably merely living on the surface and had no connection with either insect or damage.

There is left now the third possibility, i.e. that the salivary secretions injected into the tissue have a toxic effect. There are known to be two ducts (Awati (4)) down one of which there passes the salivary juices while up the other passes the plant sap, presumably mixed with some saliva. The saliva is injected under pressure by means of the very powerful pump situated in the head of the insect. After the leaf has been punctured and the insect's stylets withdrawn, a drop of fluid exudes from the hole and slowly grows in size as the cells below are killed and give up their contents. This is in marked contrast to the prick with a sterile needle or the puncture made by the harmless bugs where no drop of fluid exudes. The theory of harmful salivary injection is certainly the most probable of the three possible explanations, and further observations seem to bear this out.

The salivary glands of Capsids in general consist of a paired bilobed gland (see Fig. 4) situated in the meta-thorax one on each side, from the centre of this runs a long tube with apparently glandular walls, up to the neck where it doubles back again, ending near the gland proper in a very thin walled vesicle or reservoir which is not secretory; a second tube arises at the same point as the first and runs straight to the neck where it connects with the pump. Attempts were made to discover if any morphological difference existed between the salivary glands of *P. rugicollis* and those of other apple-feeding Capsids.

The insects were fixed in Carnoy's fluid (second formula) mostly in the early stages, or after a moult, before the chitin was hard. In spite of these precautions great difficulty was experienced in getting good penetration of the fixing fluid, and it was found necessary to detach the legs or make a small hole in the abdomen for the fixative to gain an entrance. Great care was necessary in embedding in the wax, as too long or too short a time caused the chitin to become too hard and brittle to cut. It was thought possible that the glands of *P. rugicollis* might show some extra secretory cells or that the reservoir itself might prove secretory, but no histological peculiarity was apparent, the salivary apparatus being almost identical in the various species examined, the reservoirs showing as thin collapsed vesicles.

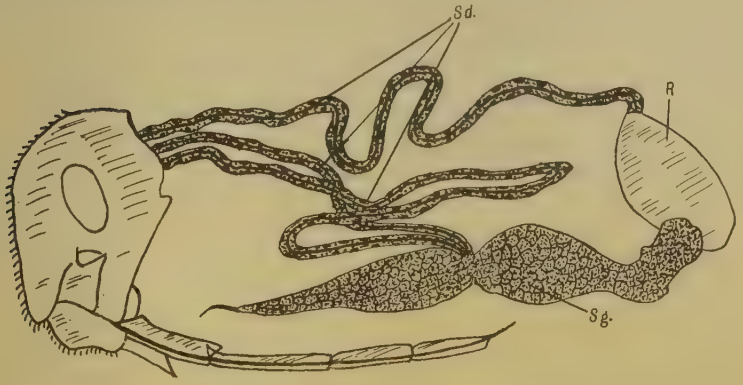

Fig. 4. Semi-diagrammatic drawing of the salivary apparatus of *Plesiocoris rugicollis*. One side only.

The fact of there being no apparent histological differences in the salivary glands of the harmless and harmful bugs does not tell directly against the theory of a toxic secretion, and all other experiments seem to point to this being the true explanation. That the damage to the cells spreads after the bug has moved to another spot, and that the mesophyll dies before the epidermis (except of course where there is a drop of sap and saliva lying on the surface of the leaf) are facts which tell very strongly in favour of this theory. Fig. 4 is a semi-diagrammatic representation of the salivary apparatus of *P. rugicollis*.

Injections were made with various dilute poisons into apple and willow leaf in order to reproduce if possible the damage caused by the bug.

(1) Dilute ammonia.
(2) Chloroform.
(3) Various dilute acids, such as hydrochloric, etc.
(4) Xylol.

In each case the leaf assumed a spotted and patched appearance, very similar to the effect produced by the Capsid, and the leaves were put back in their development to a similar extent, while if pricked with the fluid so that more than 25 per cent. of the area of the leaf was affected, the leaves died. The characteristic red spots appeared on the apple leaves and the clear patches of dead cells appeared on the willow.

The same injections were made into the apple fruit itself, the chief result being the extraordinary retarding effect on the growth of the apple; after a week or ten days the control fruit was twice to three times the size of the pricked fruit, and in many cases the inoculated specimens fell off after ten days or a fortnight.

Further experiments were made to prove conclusively if possible the harmful effects of the salivary juices of *Plesiocoris rugicollis*. A number of the harmful Capsid bugs were ground up in a sterile mortar with a single drop of sterile water and the resulting fluid injected into apple and willow leaves. At the same time and into the same trees, a similar fluid, made from harmless apple Capsids, was also injected, in each case with a sterile water control. This experiment was unsatisfactory, no conclusive results could be drawn from it. A certain amount of damage was done in each case, possibly slightly more in the case of the extract of the harmful bug than in the other, but it seems probable that the harmful substance in the salivary glands was so diluted or neutralised by the other juices of the body or by the sterile water as to lose its toxic effect.

The same experiment was repeated, this time without the sterile water but again with unsatisfactory results.

Finally the whole salivary apparatus was removed from harmful and harmless bugs and pricked into the leaf tissue. This was definitely satisfactory, as the glands of the harmful bug (*P. rugicollis*) were very much more toxic than those of the harmless bug (*P. ambiguus*) which had little or no effect. The salivary apparatus of the injurious insect was placed on a young apple leaf and a small prick with a sterile needle made through it into the tissue beneath. In an hour or two the cells underlying the gland were all killed and by the next morning 50 per cent. of the leaf was dead: a similar prick made through the glands of a harmless Capsid under similar circumstances produced no effect whatever.

As has been mentioned already in this paper the damage to the apple fruit itself is very considerable, owing to the fact that the growth of the apple is almost entirely stopped by the death of the cells of the exterior; in cases where one side only is punctured by the bug, the other side of the apple continues to grow to a certain extent thus causing a greatly distorted fruit.

Fig. 5. Section of the salivary gland of *Lygus pabulinus*, 4 μ thick, $\frac{1}{12}$th oil immersion, ocular 4.

When an apple is punctured by the harmful bug, a drop of fluid exudes from the puncture and gradually increases in size, the cells surrounding it are all killed and a corky layer is formed. To investigate this phenomenon further a number of slices of potato were put in damp chambers (Petri dishes lined with wet filter paper) and harmful and harmless bugs introduced.

The object of using potato was to produce the same reaction as in the apple, but on a magnified scale. *Plesiocoris rugicollis*, *Lygus pabulinus* (a species harmful to potato foliage, etc.) and *Psallus ambiguus* were the species used. As soon as the bugs were introduced into the petri dishes they commenced to feed vigorously on the potato slices. From the punctures made by *P. rugicollis* and *L. pabulinus* a small drop of clear fluid exudes, this drop continues to increase in size for two or three hours, by which time it has attained a maximum diameter of about 3 millimetres and become greenish in colour. This drop finally dries up and leaves a large area of blackened dead cells. When the harmless bug sucks the potato no damage is caused to the tissues nor is there any exudation of fluid.

The explanation of the appearance of the drop appears to be that the salivary injection continues to work its way in the tissue till its toxic powers are exhausted, and as each cell is killed its turgidity is lost and its contents exude, forming the large drop as described. It is a striking fact that this exudation should only occur in the case of the harmful bug.

Plate III, fig. 2 is a photograph of potato slices which have been fed upon by the bugs: A and B, by *L. pabulinus*; C, by *P. rugicollis*; and D, by *P. ambiguus*. In A, B and C, will be seen the blackened areas of dead cells round each puncture while in D, although fed upon to a similar extent by *Psallus ambiguus*, there are no harmful results whatever.

The following detailed observations were made of the feeding of *P. rugicollis* and *L. pabulinus* upon potato.

P. rugicollis. *Times after removal of stylets from puncture. Size of drop exuded, in millimetres.*

	1 min.	20 mins.	1 hr.	2 hrs.	3 hrs.	4 hrs.	12 hrs.
(1)	¼	½	¾	1½	2	2½	2½
(2)	¼	½	¾	1–1½	2	2	2
(3)	¼	¼	½	1	1–1½	2	2
Lygus pabulinus							
(1) Colourless / Green	¼	½	1½	2	3	4	4
(2)	¼	½	1	2	3	2–3	3
(3)	¼	¼	½	1½	2	2	2
(4)	¼	½	1–2	2½	3	3½	3½
(5)	¼	½	1	1½–2	3	4	4

A drop of this exudation was placed upon a young apple shoot; it was found to be decidedly toxic for after a few days the shoot died.

A control experiment of pure potato sap alone had no ill effect upon the apple leaf although left in a damp chamber with the drop of sap *in situ* for several days, thus showing that some toxin had been added to the potato sap and that some chemical change had taken place, this latter as indicated by the change in colour after exposure to the air.

The salivary glands were then taken out of the following species, *P. rugicollis*, *L. pabulinus* and *Psallus ambiguus*, and placed each on the surface of a slice of potato; in the first two cases a large quantity of fluid was produced which gradually oozed out as before, and a large patch of tissue was killed; in the third case there was no effect at all. These drops of fluid were picked up with a capillary pipette and found to be toxic to apple leaves though not apparently to fresh slices of potato.

This seems fairly conclusive evidence that a harmful substance is injected by the bug and that it must be looked for in the salivary glands.

Observations were made of *P. ambiguus* in the act of feeding. Before the stylets are inserted into the tissue the proboscis is held upwards and a large drop of saliva gathers at the end, the proboscis is then lowered and the stylets forced into the tissue through the drop of saliva deposited on the leaf. After the insect has been feeding for some time the surface of the leaf is dotted over with these drops of saliva, these eventually dry up and leave no mark or visible after effect. If these drops are picked up with a capillary pipette and injected into the leaf no damage results, which is in marked contrast with the effect of the drop exuding from the puncture made by *P. rugicollis* which kills the cells underlying it. There appears to be a slight difference in the method of feeding of these two bugs, whereas *P. ambiguus* secretes the saliva and pumps it out before piercing the leaf, *P. rugicollis* inserts the stylets first and then pumps in the saliva, the latter method certainly seems the most effective and it is difficult to account for the deposition of saliva outside the leaf unless this particular species is in the habit of producing greater quantities of the secretion than *P. rugicollis*, and pumps it into the leaf as well.

Sections were cut of tissue, fixed immediately after puncturing by the bug, also of tissue punctured by *P. ambiguus*; these sections did not prove very successful, but punctures were discovered which penetrated some distance and showed laceration of one or two cells.

It is difficult to say how harmless bugs such as *Orthotylus marginatus* and *P. ambiguus* procure their food if their salivary injection does not kill the cells as it seems impossible that the contents of the one or two cells actually lacerated by the stylets should suffice for their needs;

also, if the cells are killed, the characteristic red brown colour should be formed as it invariably is on the death of cells in apple tissue. It was thought possible that *Psallus ambiguus* injected some substance which prevented the formation of the tannin material in apple tissue, but although injections were made with various substances to try and produce this effect, e.g. acids of varying strength, etc., these attempts were unsuccessful, and almost invariably resulted in the formation of the red spots and patches except in the case of strong tannic acid which produced a hole surrounded by a pale margin.

A certain species of Jassid bug found feeding on horse chestnut and producing white spots thereon, was transferred to apple on which it produced similar white spots; apparently these cells were not dead or else, as suggested above, some substance was injected which prevented the formation of the red pigment. Lefroy and Horne(6), in their paper upon the effects produced on plants by sucking insects, put forward the theory that these white patches consist of cells filled with air. White spots are characteristic of the feeding of Jassid bugs, each plant damaged by them responding in a similar manner, at any rate in those cases of which the writer has personal knowledge, i.e. apple, pear, chestnut, and potato.

An interesting parallel case to that of the Capsids is found in the apple-feeding aphids, *Aphis pomi*, and *Aphis sorbi*; one of these has little effect upon the foliage while the other (*Aphis sorbi*) causes curling of the leaves and the formation of a very bright pink pigment which is visible on the trees from a considerable distance, and which gives to the Aphis its name of Rosy Apple Aphis. Sections through this rosy material present an appearance exactly similar to that of sections through tissue damaged by *P. rugicollis*, i.e. dead cells filled with a granular material the only difference being in the colour of the pigment.

Experiments were then made with another species of Capsid known to be harmful to other plants, this was *Lygus pabulinus*, already mentioned in connection with the experiments upon potato; it is a very common insect and does considerable damage to the foliage of currant bushes, and produces the "shot hole" effect on potato plants. A number of these bugs were taken at a very young stage and "sleeved" upon apple trees, they took very rapidly to this new food and produced on apple and willow injury absolutely identical with that produced by *P. rugicollis*; the change of food plant seemed to have no ill effect on the bugs, and they mostly became adults, very few dying.

Extracts were made of the salivary glands of this insect and injected into apple and willow, causing the same effect as that produced by the

extract of *Plesiocoris rugicollis*. It seems fairly certain that a Capsid that produces damage to one plant produces damage to every plant upon which it feeds, although this damage varies slightly according to the reaction of the plant juices to the saliva. No case was found by the writer of a Capsid that was harmful to one plant being harmless to another, and conversely the harmless apple bugs, when induced to feed upon willow, were harmless to that also.

Lygus pabulinus was found feeding upon many different plants and trees, as shown in the following list; the effect produced in each case is given.

Red Currant. Reddish white patches and puckerings of leaves. Fruit untouched.
Black Currant. Whitish patches on leaves. Fruit untouched.
Pear. Black spotting of fruit and leaves.
Apple. Red spots and patches.
Plum. Red spots and patches.
Gooseberry. Reddish white patches on leaves. Fruit untouched.
Bindweed. Clear patches of dead cells. Similar to damage to willow.
Dock. Red spots.
Artichoke. Whitish patches with crinkling.
Potato. Brown spots. "Shot Hole" effect.
Willow. Clear patches of dead cells. Compare Bindweed.

This list would apply equally well to the effects produced by *P. rugicollis*.

In all the above instances *L. pabulinus* was found feeding under natural conditions except in the case of the apple where they were "sleeved" on the tree. A number of young specimens of *L. pabulinus* were placed on small apple trees growing near some currant bushes without any measures being taken to prevent their escape; they remained upon the apple trees several days, causing a certain amount of damage, and then migrated to the currant bushes. It seems probable that if these specimens had been newly hatched they would have stayed upon the apple trees as it is quite easy to rear them under controlled conditions upon apple from early stages to adults.

An American worker, C. R. Crosby (7), records two species of Capsids, *Heterocordylus malinus* and *Lygidea mendax*, as living upon apples in America, and describes and figures injury exactly similar to that produced by *Plesiocoris rugicollis* and *Lygus pabulinus*, the two species more particularly dealt with in this paper.

An interesting point arises as to why *P. rugicollis* should have changed its food plant from willow and alder to apple, and if this species could do so why should not *L. pabulinus* do the same? It will be seen from the table of food plants that it has already a varied diet, it can also be

easily reared upon apple as shown, so that it would not be altogether surprising if another pest were added to the already very long list of those attacking and injuring apple trees.

An attempt was made to find out the nature (acidity or alkalinity) of the salivary juices of various harmless and harmful bugs. Some specimens of *L. pabulinus* and *P. rugicollis* and *Psallus ambiguus* were starved for 24 hours and then introduced into a petri dish containing red and blue litmus paper soaked in sugar solution. The bugs would not as a rule insert their stylets more than once; the result of the insertion was to leave a brown spot on both red and blue litmus paper.

SUMMARY.

There are several species of Capsid bugs which normally feed on the leaves and fruit of apple trees but only one causes any damage, i.e. *Plesiocoris rugicollis*. This species produces the death of the tissue surrounding each puncture in the leaves made in feeding and on the fruit produces great distortion and "russeting."

There are three possible explanations of this damage:

(1) A purely mechanical injury produced by the insect's stylets in process of sucking.

(2) The possibility of the bug acting as a "carrier" of bacteria and by injecting these into the plant along with the saliva so sets up a pathological state.

(3) The injection of some secretion from the salivary glands which has a violently toxic effect on the plant tissue.

It was found impossible to reproduce by mechanical means the injury resulting from the feeding of *P. rugicollis*, also the fact that the other species of Capsid bug feed in a similar manner and produce no injury militates strongly against the theory of mechanical injury only.

As regards the second theory, no bacteria could be discovered in microtome sections of either damaged plant tissue or the salivary glands of the bug, and all attempts to reproduce the damage by means of bacteria failed.

The third theory was proved to be the correct explanation by several experiments and observations.

Experiments were made to try and reproduce the bug injury with various dilute poisons; in most cases a very similar appearance was produced in the foliage, but the attempts were unsuccessful in the fruit itself with the exception of the very great retarding effect in the growth of the fruit, which is one of the results of the bug injury.

By feeding the bugs on slices of potato instead of apple the same

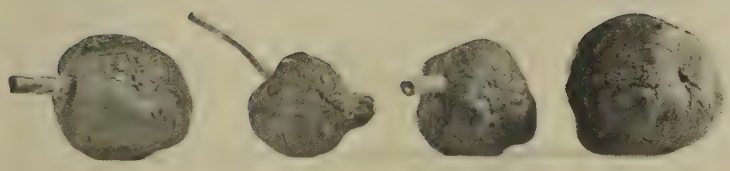

Fig. 1.

Fig. 2.

effect was produced, but on a magnified scale. The salivary glands of *P. rugicollis* and of *Lygus pabulinus*, a bug harmful to potato foliage, when placed on a freshly cut slice of potato in a petri dish, produced a violent reaction which killed much of the tissue surrounding the glands. The same experiment was carried out with the glands of one of the harmless apple-feeding bugs *Psallus ambiguus*, these had no effect whatever on the potato. When the salivary glands of *P. rugicollis* were pricked into apple buds, the shoots were killed within 24 hours. The salivary glands of *P. ambiguus* when similarly treated had no effect. Observations were made showing the rate of exudation of sap from the bug's puncture in the potato and these are given for *P. rugicollis* and *Lygus pabulinus*. A list of common plants and fruit trees with their various reactions to the feeding of harmful bugs is also given.

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EXPLANATION OF PLATE III

Fig. 1. Photograph of four apples, showing the typical damage produced by *Plesiocoris rugicollis*. Note the "scab" effect.

Fig. 2. Photograph of four slices of potato. A, B damaged by *L. pabulinus*, C by *P. rugicollis* and D fed upon by *Psallus ambiguus*, but undamaged. In A, B, note the large punctures surrounded by dead and blackened tissue.

EXPLANATION OF LETTERING.

An. Antenna. *C.R.* Collapsed Reservoir. *Lbr.* Labrum. *Lb.* Labium. *Md.* Mandibles. *Mdl.* Mandibular lever. *Md.C.* Cavity of the mandibles. *Md.H.* Hooks of Mandibles. *Mx.St.* Maxillary Stylets. *R.* Reservoir. *Sd.* Salivary duct. *Sg.* Salivary gland.

SPHAERONEMA SP. (MOULDY ROT OF THE TAPPED SURFACE).

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(With 4 Plates.)

The treatment to which the rubber tree (*Hevea brasiliensis*) is subjected in order to obtain the latex, viz. excision of bark and the major portion of the cortex in the form of thin shavings at frequent and regular intervals (this constitutes the operation known as "tapping"), leaving only a thin cover of the inner cortex overlying the cambium, is such that there is little cause for wonder when one learns that the exposed tissue is attacked by fungoid pests, some of which are capable of establishing themselves as parasites in the cortical tissue. Some indeed go further than this and pass through to the wood elements beneath and becoming firmly established there, spread up or down in a vertical direction, killing the cambium and the cortical tissues outside.

One of the most dangerous of these parasites, since it destroys the cortical tissue and thus ruins the tree so far as the production of revenue is concerned, is a species of *Sphaeronema* which is the responsible agent in causing the rotting or destruction of the tapped surface, i.e. this fungus utterly destroys the thin skin of cortex remaining after tapping, hence delaying the renewal, and in fact making it almost or quite impossible for tapping to be carried on over that section again. Normally a tapped surface can be tapped over again in from 5–6 years or even sooner, as by that time the regenerated cortex is sufficiently mature to yield an amount of latex which is remunerative.

In the *Agricultural Bulletin of the Federated Malay States*, Vol. vi, No. 1, October 1917, Messrs Belgrave and de la Mare Norris writing on Bark Cankers and their treatment, describe a bark canker as "Mouldy Rot of recently Tapped Surface." Though stating that inoculation experiments indicate *Sphaeronema* as the causal fungus they apparently had not definitely determined the point.

The disease was originally confused with another well-known and wide-spread disease of the tapped surface, viz. Black Thread or Black Line Canker the causal fungus of which is a species of *Phytophthora*, Mouldy Rot being considered a virulent form of this.

Further investigation however showed that *Phytophthora* sp. was never present in tissues affected by Mouldy Rot, species of *Cephalosporium*, *Fusarum*, *Sphaeronema* are constantly present and occasionally several other saprophytic fungi and bacteria are to be found in the tissues.

The writers commenced their investigations of this disease in December 1918 and in March 1919 issued a preliminary note on the subject (First Malayan Report, 1919, Rubber Growers' Association).

The fact that a species of *Sphaeronema* had already been suggested as the causal fungus, determined us in working first on this fungus, especially as the other fungi present in the diseased tissue are common and well known saprophytes. Attempts to isolate the *Sphaeronema* by means of pycnidiospores in the usual ways all failed, chiefly owing to the fact that they are exuded in a sticky mass, almost impossible to separate into individuals, and foreign matter, spores etc. is held tenaciously. These spore masses refused to separate in liquefied nutrient agar, and frequently were killed at the temperature necessary to keep the agar in a liquid condition.

We then tried to isolate the fungus by picking out resting spores under the microscope, but the results were not encouraging. Finally we decided to try the mycelium fairly deep in the tissues and this gave the best results in the shortest time. Experiments with inoculations of *Cephalosporium* and *Fusarium* on stripped surfaces gave always negative results.

ISOLATION OF THE FUNGUS.

Portions of old dry bark which had been affected with mouldy rot were used as the starting point in investigating this disease. A portion of bark 6 inches square was removed from a healthy tree and the underlying fresh tissue exposed. Inoculation was effected by scraping the old infected bark, mixing the scrapings with distilled water and applying with a soft brush.

At the same time the inner surface of the bark removed was inoculated similarly, cut into four portions 3 inches × 3 inches and kept under observation in covered glass dishes.

In 48 hours all the inoculated surfaces had become discoloured, turning a dirty brown, and by the end of the fifth day the cells of the

outer surfaces in all cases had been completely killed. Species of *Cephalosporium*, *Fusarium*, etc., were gradually covering the whole with white mycelium, and bacteria were completing the work of destruction. Portions of infected bark and wood were examined microscopically after 48 hours and again after six days. The mycelium had in places penetrated to a depth of $\frac{1}{10}$–$\frac{1}{8}$ inch, apparently penetrating most deeply along the medullary rays and then spreading laterally more slowly. Even in cells almost filled with mycelium, the nucleus in some cases was still present and apparently unaffected after six days, but in most cases, of the cells attacked, the contents had disintegrated or entirely disappeared. In the bark, cells containing tannin were also attacked. A few characteristic fruits (pycnidia) had developed by the end of the fifth day and quite a large number in six days, the surface where these appeared having turned quite black.

A mass of spores just emerging from the apex of a pycnidium was carefully removed on sterilised needles, the operation being conducted with the aid of a high power lens; the moulds present, *Cephalosporium*, *Fusarium*, etc., were as far as possible excluded and inoculations made on agar and on fresh bark sterilised outside with picro-formal, and then placed straight from the tree into sterilised tubes.

The bark showed the typical brown discolouration round the point of inoculation at the end of 24 hours.

One of these pieces of bark after six days growth was sterilised in 1/500 corrosive sublimate solution, then washed with freshly boiled distilled water, and finally the upper (previously infected surface) being the original inner surface of the bark shaved off with a freshly sterilised chisel. A second shaving was then taken from the surface newly exposed, this presumably contained active pure mycelium, and in fact such proved to be the case, as on being brought into contact with clean bark fresh from the tree, the characteristic colouring was apparent in 18 hours, while the controls remain unaltered. In every case of successful inoculations, the attack spread with quite remarkable rapidity.

CULTURES.

Cultures were set up from spores removed from pycnidia produced on bark as above, on Prune agar, 2 per cent. virol agar, Quaker oat agar, agar made with infusion of rubber tree bark, and in every case pycnidia were produced in abundance in from five to nine days. Similar cultures on sterilised wood produced an abundance of pycnidia and also resting spores in from 10–15 days. Cultures on 2 per cent. cane sugar agar gave very

good results. The growth on dolichos agar and on bean agar was much slower than on those previously mentioned, pycnidia however were produced even on these in about 20 days and a fair number of resting spores in the same time. In every case of inoculation of freshly exposed surfaces of bark or wood, infection was set up, and the disease rapidly spread over the entire surface exposed, more particularly when an excess of moisture was present.

In six cases portions of bark about six inches square were removed from the tree, and the exposed underlying surface inoculated with spores from pycnidia in water. When a considerable number of pycnidia had been produced on all these surfaces and they all showed the characteristic appearance of mouldy rot, jodelite was applied, and the next day a fresh portion of bark removed below, but in continuation with the first surface exposed. In every case the disease appeared on the fresh surface at the end of two days. Discolouration was apparent as a continuation from the previously affected part, the disease having spread downwards in the wood and innermost layers of bark. A similar experiment was carried out but fresh surfaces exposed laterally. The disease again spread to the freshly exposed surfaces.

Many of the cultures on artificial media produced considerable numbers of resting spores embedded in the media well below the surface. These large resting spores are produced in from 8–10 days after inoculation, and, being thick walled can withstand considerable desiccation without losing the power to germinate. Some infected material which could not be dealt with at once, was put aside in a desiccator so as to keep it as clean as possible, i.e. to prevent spores of various saprophytic fungi which are almost invariably present in the air from lodging on it. Six weeks later portions of the tissue were taken and infections obtained from resting spores, on stripped surfaces, thus proving that the extreme desiccation to which the spores had been subjected had not succeeded in killing them. They are produced in abundance on the infected surface in dry weather, taking the place of the pycnidia. The third type of spores which so far we have only found in cultures in the laboratory, is very similar in size to the pycnidiospore and is cut off directly from the mycelium. Examination of infected cortical tissue in which the disease had been present 8–10 days showed that large numbers of globules of an oily or fatty nature were present. These varied much in size and were fairly evenly distributed throughout the tissue, which had been killed by the fungus.

Cortical tissue which had been affected for a considerable time con-

tained these globules sometimes in great abundance, some of the cells being full of them. No trace of these could be seen in the cultures on artificial media, they are not present either in recently infected, or normal healthy cortex. Tissue which had been killed and partially destroyed by the *Sphaeronema* formed then a suitable nidus for bacteria which were present in abundance. One case of inoculation on a stripped surface which was kept under observation proved very interesting.

The surface was inoculated 27/11/18 and six days later pycnidia appeared. In the meantime the mycelium had spread over the entire surface exposed (about 24 square inches).

Cultures were made from pycnidiospores and the surface was then left, i.e. no fungicide was applied.

By 28/12/18, approximately a month later, healing from the edges had made fair progress and a month later still the wound appeared to be in a fair way to recovery.

More cortex was removed 2/2/19 both above and below but in continuation with the part previously exposed, and in less than four days there was the usual appearance on these stripped surfaces showing that the disease was spreading. In eight days pycnidia appeared on these newly exposed surfaces and examination of portions of wood in sections from the original surface showed that the mycelium had penetrated $\frac{1}{8}''$ and was then spreading slowly in a vertical direction.

Other cases similar to the above inoculated 5/12/18, and treated with an antiseptic cover, but in which no further surfaces were exposed, have now almost completely healed over. The cortex shows no signs of disease (9/1/20) and there is every appearance of complete recovery. Regeneration from the sides will however give a very uneven surface to tap over.

During wet weather pycnidia are produced in abundance on the affected surfaces while resting spores are not at all common. In some cases where the disease proved most difficult to keep in check during a prolonged spell of dry weather, no pycnidia were produced, but immense numbers of resting spores were formed on the surface and some were also found embedded in the tissue several cells deep. Under those conditions it is probable that the resting spores provide an even surer means of distribution than the pycnidiospores and these as well as those in the tissue are equally dangerous so long as tapping is continued, the knife then being the chief agent in their distribution from tree to tree.

The pycnidiospores are quickly killed by desiccation but the resting spores can withstand this for quite a long time.

DESCRIPTION OF THE FUNGUS.

The causative fungus is a species of *Sphaeronema* which belongs to the group *Fungi Imperfecti.*

The mycelium is dark coloured—brownish—the filaments are formed of cells varying much in length compared with the width, much branched, and under suitable conditions as regards moisture, etc. grows rapidly at the expense of the host. Normally the fruiting body, a pycnidium, is produced by the end of the fifth or sixth day after inoculation. These were produced in abundance in cultures in the laboratory in about the same period as on the trees attacked.

The pycnidium is quite characteristic and should always be looked for in supposed cases of "Mouldy Rot." A pocket lens of powers × 10 diameters shows it up quite well. When mature it is a black, flask-shaped body ·12 mm.–·24 mm. wide at the base and ·24 mm.–·9 mm. long including the long narrow neck which is ·02 mm.–·024 mm. wide. The long neck has a distinctly striated appearance due to the presence of thicker portions in the form of strands. At the apex the strands split apart somewhat from the connective tissue (see Pl. IV, figs. *a* and *b*) facilitating the discharge of masses of pycnidiospores.

The pycnidia arise directly from masses of the dark coloured mycelium, which with the black pycnidia give the infected surface a black appearance; as the attack progresses this effect is accentuated. Pycnidia are, under favourable conditions produced in immense numbers, many hundreds being crowded together in quite a small area. The pycnidiospores are produced in the base of the pycnidium, and in a sticky matrix are gradually forced up and out of the neck, adhering when freshly exposed as a white, more or less globular, sticky mass, which rapidly turns brown when dried.

Eventually the mass is pushed over the side and remains sticking to the outside of the neck, being followed in a very short period—24 hours or more—by a second mass. The masses of pycnidiospores are very quickly affected by desiccation. By the time the mass has turned dark brown, it may be quite a short time after expulsion from the pycnidia, they have lost all power of germination, hence a dry season helps greatly in controlling the disease while a wet one makes it more difficult. This has however proved not always to be the case, as in some cases immense numbers of resting spores are produced when pycnidia are altogether absent during a dry period. The individual pycnidiospores 2·5 microns × 4 microns are slightly attenuated and rounded at the ends. When fresh they germinate almost immediately on a suitable medium,

e.g. a fresh surface exposed by tapping. Besides these, two other kinds of spores are produced, one being a large, almost spherical, thick walled resting spore 10–20 microns in diameter (the great majority are 10–14 microns in diameter) produced at the ends of short lateral branches, especially on the mycelium at or near the surface (see Pl. IV, fig. *c*). Cases have been observed where these spores were produced on the mycelium embedded in the tissue several cells deep, and in the particular cases observed pycnidia were scanty or entirely absent (see Pl. V, fig. *a*).

From the experiments and field observations it would appear that with a high percentage of humidity pycnidia will usually be produced very quickly in large numbers, while under dry weather conditions the resting spores are produced sometimes in almost equal abundance. It follows of course that weather conditions cannot be relied on as an aid in checking or eradicating the disease.

Deep tapping undoubtedly aids in the thorough establishing of the fungus in the tissues since under those conditions penetration to the wood is quickly effected.

Much wounding during tapping also aids in a similar way.

SYMPTOMS OF ATTACK.

A freshly exposed surface of *Hevea* attacked by *Sphaeronema* turns darker in colour than normal in quite a short time (24 hours). In three days the infected surface rots, and various species of saprophytic fungi make their appearance on the dead tissue, the presence of these being indicated by the tell-tale more or less complete cover of white mycelium. This appearance is most noticeable one to two inches above the cut. Portions of the tapped cortex sink in, forming depressed patches of various sizes, which may in a bad case extend the whole length of the cut. The affected portion frequently turns quite black. Later, in neglected cases, the fungus penetrates the wood $\frac{1}{12}''$–$\frac{1}{8}''$, spreading vertically up and down the wood fibres.

The less serious cases where only small portions of the cortex become depressed resemble Black Line Canker, but usually pycnidia may be found, sometimes in considerable numbers.

The damage caused by this disease when neglected is probably greater than that due to any other bark disease of *Hevea*. The disease continues as long as tapping is continued and is easily spread from tree to tree by the knife.

Cortex destroyed by *Sphaeronema* is frequented by small Diptera

and beetles both of which are liable to spread the disease especially by carrying the pycnidiospores which adhere to the legs and bodies.

Since the fungus quickly produces spores (5–6 days) once a tree is attacked and the initial attack overlooked, the spread of the disease is usually very rapid and whole tasks of 300–400 trees may be affected in the course of a week or fortnight.

The rapidity of spread and the short time in which it kills the tissues make this a most dangerous disease. A week may see the number of infections increased by hundreds.

The loss sustained by an estate affected by Mouldy Rot, unless efforts are at once made to obtain control and eradicate the pest, may be very great, as once it becomes fairly widespread tapping must be stopped for periods varying from 2–6 months and this may have to be repeated after reopening if the disease shows signs of reappearing. The distribution of remaining cortex after tapping also is bound to be serious if it continues for any length of time since a shortage of bark means loss of revenue.

When reopening trees after a period of rest due to Mouldy Rot the new cut if in the same section should be 4 inches below the old one; it is better to open up a new section and keep a sharp watch for any new infection which should be dealt with vigorously.

Two other species of *Sphaeronema* have been seen frequently by the writers growing as saprophytes on dead *Hevea* timber; one often appears on the cut surfaces of fresh timber during felling. These are always accompanied by hosts of small diptera which apparently find the sticky masses of pycnidiospores an attraction. Both these species produce fruit (pycnidia) viz. quickly, one of them usually in about three days or even less.

We are indebted to the Rubber Growers' Association for permission to publish the results of this work carried out on their behalf.

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First Malayan Report 1919. Rubber Growers' Association, *Kuala Lumpur*, F. M. S., March, 1919.

Third Malayan Report for 1919. Rubber Growers' Association, *Kuala Lumpur*, F. M. S., December, 1919.

DESCRIPTION OF PLATES

PLATE IV.

Fig. (*a*) Pycnidium and mycelium of *Sphaeronema* sp. Note the mass of spores at the apex of the pycnidium. × about 60.

Fig. (*b*) Apex of pycnidium showing spores and strands. × about 190.

Fig. (*c*) Resting spores of *Sphaeronema* sp. These occurred commonly during a prolonged period of dry weather when no pycnidia were produced. × about 130.

Fig. (*d*) Section of infected tissue showing pycnidia and resting spores on the outer surface. × about 32.

PLATE V.

Fig. (*a*) Section of infected cortex showing resting spores formed within the tissue. × about 200.

Fig. (*b*) Section of wood showing the mycelium of the fungus in the cells. Nuclei are still present in some cases, the rest of the cell contents being destroyed. × about 225.

Fig. (*c*) Resting spores produced on artificial medium (nutrient agar jelly) after 8 days. × about 100.

Fig. (*d*) Mycelium in cells of diseased cortex. × about 200.

PLATE VI.

Fig. 1. Recently tapped surface (A) attacked by the disease.

The white felt-like masses of mycelium of saprophytic fungi, chiefly Cephalosporium, are irregularly distributed over the decayed surface. The real cause of the disease is more deeply seated and is spreading downwards keeping pace with the tapping. The cortex B–C had been treated with an antiseptic tar mixture several times. Portions of the exposed wood so treated (D) some considerable time after treatment showed irregular white patches. These were due to a granular deposit the result of some chemical action, of the disinfectant cover on the tissues.

Figs. 2 and 3 illustrate the effect of mouldy rot on a freshly stripped surface. Two portions of cortex were stripped at the same time.

(*a*) Was inoculated with spores of *Sphaeronema* in distilled water, the spores being placed on the surface with a soft brush.

(*b*) Was not inoculated (control).

Fig. 2 shows the appearance 24 hours after inoculation.

Fig. 3 shows the appearance six days after inoculation.

Within six days the *Sphaeronema* had produced pycnidia. It will be noticed that on the infected surface, the cortex is utterly destroyed down to the wood. Saprophytic fungi are present on the decayed tissue. × about $\frac{1}{6}$.

PLATE VII.

Fig. 1. Tapped cortex of *Hevea* attacked by mouldy rot. The disease which started at A followed the tapping down to B and is still continuing.

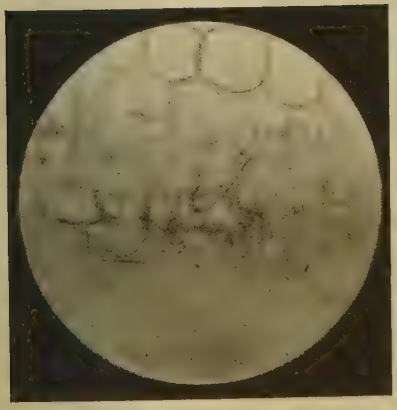
Fig. 2. Extension of the disease to new cuts. The disease had almost completely destroyed the tapped surface A–B (over 3 feet). A new cut was then opened at C on a new portion, infection quickly followed because the disease was still carrying on all round in other trees. The new infection is as previously keeping pace with the tapping (C–D).

Note the large open wounds on the surface A–B, and C–D will show a repetition of this. When the new cut started at C is finished, there will be no tappable cortex left below 4 ft. from the ground.

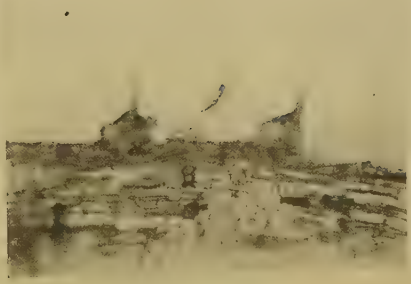
(a)

(b)

(c)

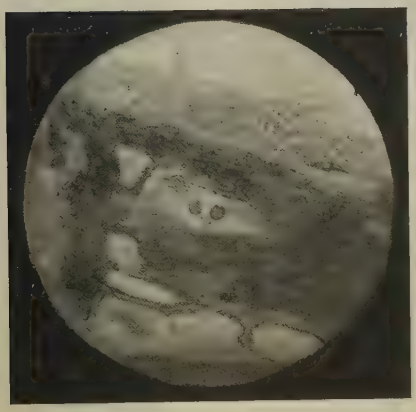


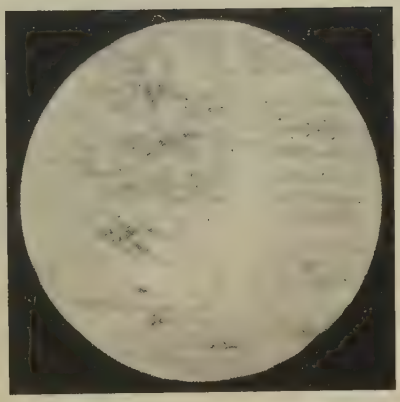
(d)



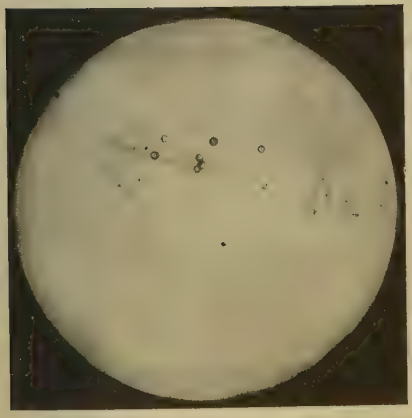
Sphaeronema sp.

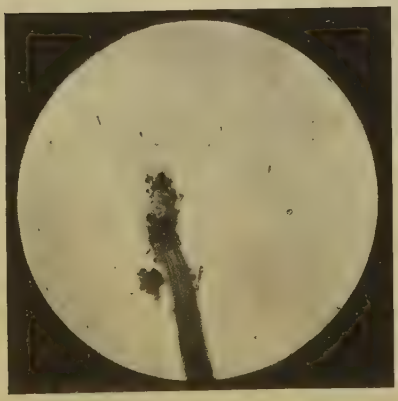
(*a*) (*b*)





(*c*) (*d*)





Sphaeronema sp.

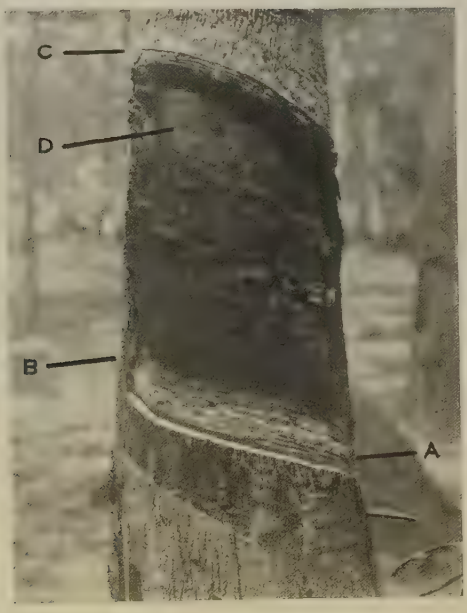


Fig. 1.

Fig. 2.

Fig. 3.

Sphaeronema sp.

Fig. 1.

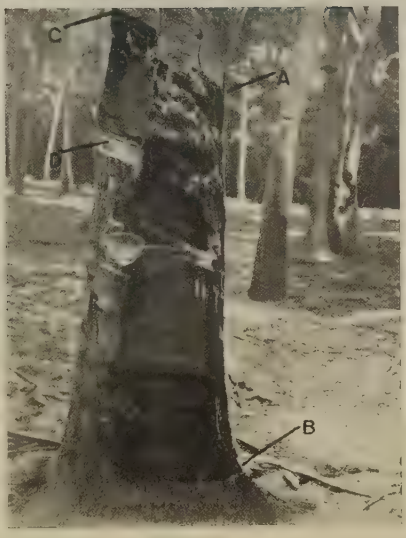


Fig. 2.

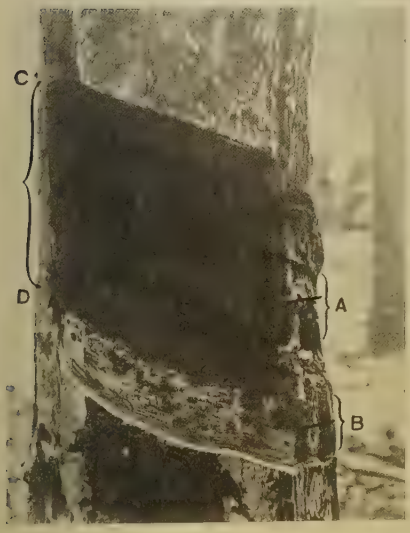


Fig. 3.

Fig. 4.

Sphaeronema sp.

Fig. 3. In this specimen 20 inches of bark have been removed on the new cut. Fifteen inches of tapped surface is almost completely destroyed. The lowest five inches (B) shows the disease is still present in a virulent form.

Note the portion (A) where open wounds extend across the tapped surface.

The portion C–D had been treated (too late) several times with an antiseptic cover.

The fungus is present in the wood and has already passed below the present cut, hence the disease will persist so long as tapping continues. The tree figured was one similar to that in fig. 2. The whole of one tapped surface (over 3 ft.) was completely ruined, and the second cut, which showed infection almost immediately after opening, is merely a repetition of what occurred on the previously tapped surface.

Fig. 4. Photograph showing tapped surface and tapping cut of a normal 15 year old *Hevea* tree unaffected by disease.

THE HABITS OF THE GLASSHOUSE TOMATO MOTH, *HADENA (POLIA) OLERACEA*, AND ITS CONTROL.

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(With 3 Plates and 4 diagrams.)

CONTENTS.

	PAGE
1. Introduction.	66
2. Characters, Life History and Habits . .	67
(i) The Moth	68
(ii) The Egg	71
(iii) The Larva	71
(iv) The Pupa	77
3. The Infestation	81
4. Origin and Method of Dispersal . . .	84
5. Control	87
(i) Spraying	88
(ii) Larva trapping	93
(iii) Moth trapping	94
(iv) Destruction of Pupae	98
(v) General Precautions . . .	100
6. Apparatus and Materials required for Control .	100
7. Summary	100

1. INTRODUCTION.

Hadena oleracea appears to have been first noticed as a pest of tomatoes grown under glass about 30 years ago at Enfield Highway. Since that time it has spread throughout the whole of the Lea Valley, the most important of the tomato-growing centres in England. In recent years it has become very serious at Worthing and at Harpenden, and it has also been noticed in Denmark, where it has not yet become a serious pest.

The destruction of the foliage by the larvae is considered to be of less importance than their habit of feeding on the fruits, and biting into

the stems of the plants. It is no uncommon thing to find three or four fruits on a truss thus destroyed by a single larva in a night. One grower had three tons of fruit destroyed by this means out of a total crop of 40 tons in the season. Another, who grows an acre of tomatoes, estimates that the pest cost him £150 in the present year, in spite of the fact that he partially controlled it by spraying. In a recent year the damage in the Lea Valley alone was estimated at £30,000, but when the cost of picking off the larvae by hand is added to this it is certainly an underestimate. In some cases the whole staff of a nursery have had to be occupied on this work, to the neglect of other duties, in order to bring the pest within bounds.

The Experimental Committee of the Lea Valley Tomato Growers Association therefore approached the Director of the Rothamsted Experimental Station with a view to the provision of an Entomologist to investigate the habits of the moth and to indicate means of control. Experiments were carried out in a large trade nursery, and laboratory work was done at the Cheshunt Experimental and Research Station. The thanks of the entomologist are due to the President of the Association, Mr H. O. Larsen, J.P., for his unfailing assistance in the conduct of the experiments in his nursery, given often at considerable inconvenience; to Mr A. Bacot of the Lister Institute of Preventive Medicine, who has helped greatly with his wide knowledge of the habits of the British Lepidoptera; also to Dr A. D. Imms, Chief Entomologist of the Rothamsted Experimental Station, who has been frequently consulted.

This report embodies the work done from the middle of April to the end of September.

2. CHARACTERS, LIFE HISTORY, AND HABITS.

The species is common and generally distributed throughout the British Isles to the Shetlands, the greater part of Europe, and also occurs in Asia Minor (Meyrick). The moth normally flies in June and July, with sometimes a partial second brood in the autumn. The larvae feed on a wide variety of low plants, and on certain shrubs and trees. In the neighbourhood of the nurseries they have been observed out of doors on *Polygonum, Chenopodium, Rumex* and *Brassica*, and on one occasion on tomato. The eggs were found on nine occasions on *Chenopodium*, but were not observed on any other plants.

(i) The Moth.

The moth measures $1\frac{1}{2}$ to $1\frac{3}{4}$ inches (35–40 mm.) across the wings. The fore wings are purplish brown, sometimes brownish drab, with a few scattered white scales. The first and second lines across the wings are very faint and there is a fine well-marked white subterminal line provided with two sharp median tooth-like projections. The orbicular and reniform stigmata are usually whitish edged, the former bearing a yellowish spot in its centre. Hind wings greyish, usually with a fuscous discal crescent and a posterior clouding or suffusion. There are no sexual differences in the markings. The general appearance of the insect may be gathered by a reference to South's *Moths of the British Isles*, Vol. I, Pl. 120.

The females largely outnumber the males. From among 152 moths bred from pupae in the laboratory, 103 (68 per cent.) were females and 49 (32 per cent.) were males: out of 1230 trapped in the greenhouses 872 (71 per cent.) were female and 358 (29 per cent.) male. The sexes were distinguished by squeezing out the genitalia after death. The proportion of females is therefore about 70 per cent., and as in cages where the moths were kept in their natural proportions practically all the eggs were fertile, it must be assumed that one male can fertilise several females.

The moths in the greenhouses hide under clods of earth or amongst the mulch, sometimes in dark places under the gutter-boards and occasionally on the undersides of the leaves. They are rarely seen by day except when they are disturbed by watering. They commence to fly at dusk and may then be seen beating along the glass and endeavouring to escape. Sometimes they work along cracks where fresh air flows into the houses and attempt to force their way through. This attempted and partially successful emigration of the moths is probably due to a dislike for the atmosphere of the houses, as other species which pass in by accident behave in the same way. These activities draw a large proportion of them to that part of a block of glasshouses which is most strongly lit at dusk, and thus an end house of a block, or the ends of all the houses along one side, become more heavily infested with caterpillars than the other parts. These heavily infested parts, in the cases which have been investigated, have always been found to be towards the south-west. Additional evidence of this is afforded by the following facts. In systematic trapping by means of 36 traps, evenly distributed through a block of 12 houses over a long period, 1444 moths were caught in the 12 traps along the southern side upon which the light at sunset

fell (the west end being shaded by a grove of trees) while only 956 were taken in the 12 traps on the northern side, which was darker at dusk. In the trap in the south-west corner of the block 194 moths were caught, a number which is more than double the average catch (80) of all the traps exposed during the same period.

The moth commences to lay eggs on the second or third day after emergence from the pupa. Sometimes the eggs are laid singly, but usually they are placed in large batches. The moth first lays a well-ordered layer which is distinctly arranged in rows of four. On these a second smaller layer is often placed, and sometimes a third layer is added, when the patch of eggs appears to be a disordered heap. The number of eggs laid in a batch varied up to a maximum of 325, the average number in a hundred batches being about 66. They are almost invariably placed on the lower surfaces of the leaves. On only one occasion has a batch been found on the upper surface.

The moth is long lived, especially if food is obtainable, and its egg production is greatly increased by feeding. Both sexes feed eagerly on the juice of broken ripe tomato fruit, and as these are carelessly left to rot in many nurseries this food is of easy access to them. Even without food however the moth is a prolific one, as the following experiments show.

Table I. *Showing the effect of supplying broken ripe tomato as food to the moths in captivity.*

	Moths fed	Moths not fed
Number of moths employed	22	28
Number of males	5	9
Average life	21 days (12 to 28)	10 days (5 to 15)
Number of females	17	19
Average life	19 days (9 to 29)	11 days (6 to 16)
Total eggs laid	190 batches	91 batches
Average batches per female...	11·2 batches	5·3 batches
Average eggs per batch ...	78	55
Average total eggs per female	872	263

Moths were enclosed in two cages constructed of a frame-work of wood, with three sides and the roof of muslin, and one side of glass; the dimensions being about 18 in. × 18 in. × 2 ft. high. Tomato or other plants in pots were placed in these. In one cage a broken ripe tomato was supplied, and in the other a dish of water but no food. The moths were placed in the cages on the day of their emergence, and the length of life was found by noting the dates of their deaths. The number

of batches of eggs laid was counted, and counts of the eggs were made from 50 batches removed at random from each cage. The results are shown in Table I.

A fed female moth on the average survived a month and produced nearly 900 eggs. Under more natural conditions the number is probably greater. Access to food doubled the average life of the moths and the average number of batches of eggs laid. It increased by 33 per cent. the average number of eggs in a batch, and a fed female produced more than three times the number of eggs laid by an unfed one. A repetition of the experiment gave similar results: six fed female moths, with an average life of 14 days, laid 66 batches of eggs, and seven unfed females, with an average life of six days, laid 13 batches.

Table II. *A study of the selection of the food plant by the moth.*

Series	I	II	III	IV	V
Total No. of batches of eggs ...	68	41	74	78	71
Plant	Percentages of batches				
Tomato	4·4	25	38	18·2	31
Chenopodium album (White goosefoot)	38·2	37	62	—	69
Urtica dioica (Stinging nettle)	1·5	—	—	19·2	—
Solanum dulcamara (Bittersweet) ...	8·5	13	—	15·4	—
Senecio vulgaris (Groundsel)	4·4	—	—	15·4	—
Convolvulus arvensis (Bindweed) ...	4·4	—	—	—	—
Rumex acetosella (Dock)	4·4	—	—	11·5	—
Taraxacum officinalis (Dandelion) ...	5·9	—	—	—	—
Plantago major (Plantain)	10·2	13	—	1·3	—
Lamium purpureum (Dead nettle) ...	0	—	—	20·5	—
Polygonum aviculare (Knotgrass) ...	5·9	—	—	0	—
Lettuce	8·8	14	—	—	—
Cabbage	1·5	—	—	—	—
Radish	0	—	—	—	—

Experiments were carried out in similar cages to discover (1) whether the moth has any preference for one plant over another in selecting foliage on which to lay eggs; and (2) whether it would be possible to attract them from the tomato plants in the glasshouses by planting any particular weed amongst the rows. If such attractive weeds were discovered great benefit might accrue, since they could be sprayed with a poisonous spray throughout the season. Various common garden plants and weeds were planted in pots and boxes, and placed in the cages, where their positions were interchanged every day or two. As far as possible an equal amount of foliage of each variety of plant was included. The moths used were all bred from larvae collected on tomato

plants in the nurseries. Five experiments were carried out, in which about a hundred moths were used. The batches of eggs were removed and counted every few days. The results of the experiments are shown in Table II, in which the percentages of the batches of eggs laid on the various plants in each trial are given.

Whenever the common weed "white goosefoot" (*Chenopodium album*) was included, the moths showed a distinct preference for it over the other plants. This preference appears to be about two to one as compared with tomato when equal foliage is exposed. The attraction is insufficiently powerful to give appreciable benefit, since a trap crop could not be a bulky one. Experience subsequently gathered in the nurseries confirms this. *Chenopodium* is a common weed in the houses and, where the infestation is heavy, it is stripped of its foliage by the larvae. Where the infestation is light, it is rarely discovered by the moths. No experiments on a practical scale were therefore carried out on these lines.

(ii) The Egg.

The egg is flattened and strongly ribbed, without any distinctive markings. Its colour varies at the laying through various shades of green to almost white. During incubation it becomes yellow, and a few hours before hatching, it turns black owing to air entering the shell. The eggs hatched in seven or eight days at mean temperatures varying from 67 to 80° F. All the eggs in a batch hatch within a few hours.

(iii) The Larva.

The newly hatched larvae eat part of the egg shells and then commence to feed on the lower surfaces of the leaf on which the eggs were laid. They do not eat completely through the leaf until they are more than a week old. They feed mainly during the night and remain quiescent on the plants in the daytime. At first they drop readily by threads if disturbed, but later this habit is lost. During growth they cast their skins five times, a sixth moult taking place at the pupation.

In its first three skins the larva is always green and may retain this colour throughout its active life. In other cases at the fourth or fifth moult it may take on a lighter or darker shade of brown, and occasionally it becomes somewhat reddish. Yellow larvae and some almost white have also been seen. The skin is closely speckled with white spots, and the hair bases appear as conspicuous black spots on the back and sides. The spiracles are white, with a black spot before and behind,

and lie in a bright yellow line which runs the whole length of the body. A line above this, and one along the centre of the back, vary in colour according to the food, as they are merely transparent patches of the skin through which the gut shows: they are usually dark grey. The green and brown forms of the larvae are figured by Buckler, *Noctuae*, Vol. III, Pl. XCIV.

The larvae proved difficult to rear on a diet of tomato foliage alone (Comet variety), though little difficulty was experienced when they were fed on certain other foods. When they hatched on growing tomato plants in large airy cages they scattered from their food in a few days and were unable to find it again. It was necessary to keep them in close contact with the foliage. The most satisfactory method was to place not more than three together on the food plant between plugs of cotton wool in narrow test tubes, and to transfer them to larger tubes as they got older, replacing one of the plugs by a muslin cover. In their last stage they were generally transferred to small plant pots containing earth, and closed by muslin covers. The food was renewed every day or two. In other cases they were sleeved on the growing plant.

Even when these precautions were taken only very small percentages, at most attempts, reached maturity, and in several instances every individual of a batch died. Only once was a large proportion of a batch successfully reared on tomato foliage. Those which succumbed simply ceased to feed and died, unless a change of food was supplied to them. In most cases no recognised disease appeared among them, though the common "flacherie" disease occurred in some. A larva which dies of flacherie has a very characteristic appearance. It becomes an unhealthy white colour, and is soft and readily ruptured if touched. It ceases to feed and remains clinging to the plant by its prolegs. The following day it turns black and falls away in greyish fluid drops. The disease is tolerably common in the houses.

Three of the experiments in rearing will be given in detail.

(*a*) A batch of 135 eggs, laid by a moth reared from a larva collected in a greenhouse, was placed on tomato foliage on beaten earth in a small glass jar covered with muslin. On the fourth day after hatching six of the larvae were isolated in test tubes, and of these, one escaped, three died, and two reached maturity and commenced to spin up on the 35th and 38th days of active life respectively. The pupae were small but healthy, and produced perfect moths. (Of 21 larvae reared on knotgrass under precisely similar conditions, 20 became mature between the 29th and 33rd days of life, and only one died.) The re-

maining larvae of the batch were kept in the jar and were supplied with fresh tomato foliage every day or two. No disease was apparent, but on the 14th day 25 only remained alive; on the 23rd day 16; on the 38th day, 3, which were all very small. On the 52nd day one was still alive but was very feeble and not one-third grown. It had apparently not fed for some days and appeared to be dying. It was still kept in the same jar and was supplied with knotgrass. The following day it was seen to be feeding on this, and a week later was growing fast. On the 75th day after leaving the egg it became mature and began to spin its cocoon. It was then perfectly healthy and weighed ·96 g., a weight which is above the average of the mature larvae.

(*b*) A small batch of eggs, laid by a moth obtained from the tomato houses, was divided into four equal parts, each part containing about 15 unbroken eggs. When these were about to hatch they were placed on four plants growing in pots, enclosed in muslin sleeves, and kept on the ground in the tomato house. The plants used were knotgrass (*Polygonum aviculare*), white goosefoot (*Chenopodium album*), bittersweet (*Solanum dulcamara*), and tomato. (The bittersweet is the commonest weed in the tomato houses, and one upon which the moth frequently oviposits. The foliage often shows marks where the larvae have fed, but they are very rarely found upon it.) The larvae were transferred to fresh plants during their growth when necessary. After the first week of life they were removed every day or two and weighed, the average weight of those on each plant being plotted in a diagram. The history of these four lots of larvae is as follows:

1. On knotgrass 12 larvae commenced to feed. Their growth was rapid and uninterrupted. One was accidentally crushed and the remainder attained maturity between the 20th and 22nd days of active life. Their growth is represented by the dotted line in Diagram I.

2. On goosefoot nine larvae commenced to feed. Their growth was rapid but rather less so than on knotgrass. Two died without any disease being apparent. The flacherie disease appeared among them and five died of this, two pupating on the 23rd and 27th days of active life.

3. On bittersweet ten larvae commenced to feed and survived the 15th day, growth being very slow but rather more rapid at first than on tomato. They then began to die off though there was no apparent disease. On the 28th day one only survived, and had a weight of ·08 g.; on the 29th day, ·07 g.; on the 30th day, ·055 g. Like the rest of this batch it was apparently starving to death, and though it was transferred

on the 30th day to knotgrass it was too feeble to feed and died the following day.

4. On tomato 12 larvae commenced to feed and growth was very slow. On the 26th day two only remained alive. Of the rest one had died of the flacherie disease and the others of no apparent disease. Of the survivors on this day one weighed ·06 g. and the other ·11 g. The smaller one, which experience showed would have died on a tomato diet, was transferred to knotgrass, and in nine days it outstripped the larger one and then grew rapidly and uninterruptedly, pupating with a weight of ·94 g. on the 50th day of active life. The growth of this larva is represented in Diagram I by the broken line from the point

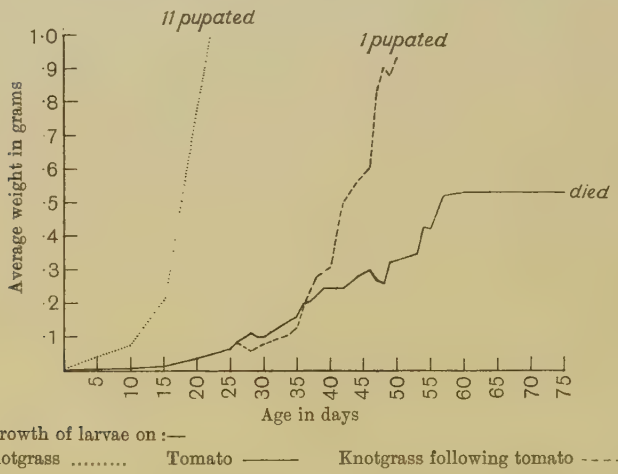

Diagram I. Contrasting the growth of a batch of larvae on *Polygonum* and Tomato.

where it was transferred from tomato. The remaining one continued to grow slowly on a diet of tomato foliage till the 46th day, when it ceased to feed for two days and lost weight. A ripe tomato fruit was then supplied to it and it fed readily on this for a few days, subsequently feeding alternately on foliage and fruit. It was not weighed after the 57th day but it was seen to be feeding little and died on the 76th day. The growth of this series fed solely on tomato, is shown in Diagram I by the continuous line, and is in striking contrast to the development on knotgrass.

(*c*) A small batch of eggs, found on *Chenopodium* growing on a rubbish heap in a nursery, was divided into two parts, half being placed

on cut *Chenopodium* and half on cut tomato foliage, in glass tubes in a tomato house. Six larvae commenced to feed on the *Chenopodium* and grew rapidly, all maturing between the 24th and 28th days of active life. Their growth is represented by the dotted line in Diagram II. Eight larvae commenced to feed on the tomato foliage, and two of these died without showing signs of disease. The remaining six became mature on the 34th and 35th days. Their growth is represented by the continuous line in Diagram II. Though the development was uninterrupted it occupied on the average nine days longer than on *Chenopodium*.

Larvae were reared from the egg on *Polygonum* and *Chenopodium* and transferred in various stages to tomato foliage and fruit. In ten

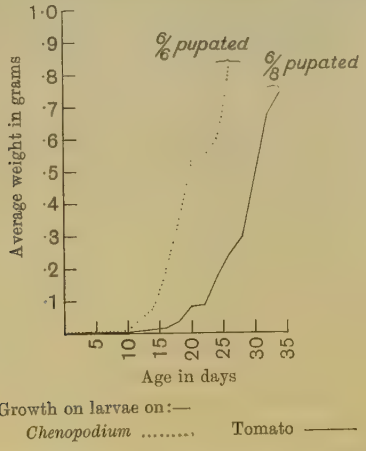

Diagram II. Contrasting the growth of a batch of larvae on *Chenopodium* and tomato.

experiments, 110 larvae, from two to three weeks old, were used in this way. None of these reached maturity, though many of them fed and some made considerable progress. It was not concluded that the larvae in the houses could never pass from these weeds to tomato, but only that such transfer would not be common. On the other hand larvae collected from tomato were very frequently transferred to a diet of *Chenopodium*, *Polygonum*, *Rumex*, cabbage and lettuce, on which foods they invariably matured normally.

These experiments are sufficient to show that in some way a diet of tomato foliage alone is not suited to the majority of the larvae, which therefore require a change of food before they can mature. There is

also considerable variation in this respect among different batches, and among the individual members of a particular batch. The same phenomenon has been met with rarely in larvae confined to a diet of *Chenopodium*, since occasionally one apparently starved though food was abundant, and conditions healthy. It is of interest that the only other case when an attempt at breeding from the egg failed entirely was on another Solanaceous plant, *S. dulcamara*. This suggests that the heavy death rate on tomato may be due to one or other of the poisons which are characteristic of this group of plants, and to which the majority of the larvae may be not immune. On the other hand the recoveries of the larvae which were transferred from tomato to *Polygonum* recall strongly the recoveries of beri-beri patients when they are supplied with a diet containing the vitamines deficient in their former food. The large death rate may be due to a deficiency in tomato foliage of some substance essential to the maturing of the larvae.

Whatever the cause of this phenomenon it adequately explains why the larvae, though surrounded by abundant tomato foliage in the glass-houses, often leave it and feed on the hard green fruits, and bite into the stems and eat along the pith, in their search for a more suitable diet (see Pl. VIII, figs. 1 and 2). It explains also why the tomato crop in the heavily infested nurseries has not been entirely destroyed. As will be shown presently there are two complete generations and a partial third in the tomato houses in the season, and the offspring of a single pair of moths, emerging in April, might be nearly half-a-million caterpillars in the second generation in August, if all survived; or an average of 30 to each plant over an acre. Such numbers have of course never been attained in any nursery, and as the moths emerge by the hundred to an acre in the heavily infested houses in the Spring, the death rate of the larvae during growth must be enormous. Apparently the young ones scatter in very large numbers from the tomato plants in searching for more suitable food and most of them fail to regain the plants.

The larvae have been successfully reared on *Polygonum* in a cucumber house, but two attempts to rear them from the egg on cucumber foliage failed. In one of these cases 14 larvae from a batch of about 100 eggs passed the first moult and lived eight days, but none survived the second moult and they were all dead on the 11th day. Twenty half-grown larvae which had been collected from tomato plants were fed on cucumber foliage. One of these became a small healthy pupa on the 22nd day after commencing the cucumber diet, two others were then alive but died on the 28th and 29th days respectively, apparently of

starvation. The conclusion drawn was that the moth could pass through its life history in a cucumber house if weeds were allowed to grow there, since in all its stages it can survive the high temperature and humidity.

Table III shows the effect of the various food plants employed on the duration of the active life of the larvae, only those which were confined to one diet, and which formed healthy pupae, being included. It shows also that the higher temperatures of the tomato houses increase the rapidity of the development on each food. The average life of the larvae in the houses under natural conditions, estimated by regular counts of them at different stages, appears to be between 35 and 45 days.

Table III. *Showing the effects of various foods and temperatures on the duration of the larval life.*

Dates	Place	Temperatures mean	Temperatures range	Food	Number of larvae	Life in days average	Life in days max.	Life in days min.
16. v.–15. ix.	Laboratory	66°	50–83°	Tomato	6	39	44	37
				Chenopodium	16	30	34	28
				Polygonum	20	31	33	29
				Rumex	3	32	33	31
12. vi.–8. ix.	Tomato House	72°	52–94°	Tomato	8	35	41	27
				Chenopodium	11	28	35	25
				Polygonum	11	22	23	20
13. viii.–6. ix.	Cucumber House	81°	60–112°	*Polygonum*	9	25	26	24

(iv) The Pupa.

When full-fed the larvae seek out moderately dry places in which to pupate. Experience in the nurseries shows that they will travel considerable distances in search of suitable sites, and will spin up in crevices in the walls and woodwork, and in sacking, or sometimes among the leaves of the plants. On a heavy wet clay soil most of them pupate in the structure of the glasshouse, but where the soil is light and friable the majority pupate there, especially under the pipes or round the concrete piers. The pupae are frequently found in the mulch, or just below it, and very rarely indeed at a greater depth in the ground than one inch. They are often seen in the unfaced joints of the pipes, and in the tops of the canes used for plant staking. In such places the larvae spin light silken cocoons and remain quiescent for two or three days before pupating. The pupa is smooth, shining, and normally almost black, though occasionally lighter specimens are seen.

The period during which the insect remains in the pupal stage varies

very considerably. It is known that in nature there is often a partial second flight of this moth in the autumn. This is derived from the larvae which become full-fed in July and August, some of which produce moths in three or four weeks in warm years, while others do not respond to the favourable temperatures but remain as pupae till the following summer. If the autumn proves unfavourable to the second flight and none of their offspring survive to maturity, those which have not emerged carry on the species the following year. Although the temperatures in the tomato houses are fairly equable from the beginning of spring to the end of autumn the same phenomenon is seen and the response of the pupae to the favourable temperatures varies.

The history of the pupae which were observed in the tomato house and the laboratory is given in Table IV. Those which were kept in the greenhouse were in the shade under the staging and were, for the most part, on moist soil in glass jars. A thermometer was kept among them and the temperatures were recorded daily. Those in the laboratory were in similar jars out of the sun. The table shows the mean, absolute maximum and absolute minimum temperatures for each month. It also shows the number of pupae which pupated in each month; the numbers of these from which moths emerged after shorter or longer periods, with the possible limits of these periods in brackets; and a note on the pupae not accounted for in the previous columns. It will be seen that the pupae in the laboratory behaved similarly to those in the greenhouse, in spite of the fact that they were exposed to somewhat lower temperatures. On the average the pupation period in the laboratory was slightly prolonged, and it was evident that there is some factor in addition to temperature which partially influences the period. An account of those kept continuously in the tomato house follows.

None of those which pupated at the end of April produced moths in the shorter period, but most of them emerged in a period varying from 100 to 200 days. All but one of those which pupated in May emerged in a short period (17–31 days). The one which delayed its emergence in this month became a moth about the 122nd day. All those which pupated in June became moths after a short time (20–50 days), but took on the average rather longer than the May pupae. This was probably due to a spell of cold weather at the end of the month when the temperature in the greenhouse fell to 54° F. on several occasions. Prolonged pupation was again in evidence among the July pupae, as three-quarters of them emerged in less than 35 days, and the remainder have not produced moths up to the end of November, 120–150

days after their pupation. In August only 17 per cent. emerged in the short period (17–32 days), and 83 per cent. are still pupae after 90–120 days. These were exposed throughout the first 60 days after their pupation to a higher temperature than those which pupated in the laboratory in June, though the latter all emerged in the short period. None of those which pupated in September have yet produced moths.

Table IV. *Showing the behaviour of the pupae from April to November, and the partial influence of temperature on the pupation period.*

	Month	Temperatures Mean	Temperatures Range	No. of pupae	No. of moths which emerged after Short period	No. of moths which emerged after Long period	Nos. which remain pupae, or died
Tomato House	April	—	—	11	0	10 (102–200 days)	1 after 200 days
	May	73·2°	58–89°	85	82 (17–31 days)	1 (122 days)	2 died
	June	70·9°	54–90°	65	63 (20–50 „)	0	2 died
	July	70·8°	54–90°	30	23 (16–35 „)	—	7 after 120–150 days
	August	71·3°	52–94°	110	37 (17–32 „)	—	73 „ 90–120 „
	September	70·7°	52–90°	15	0	—	15 „ 60–90 „
	October	63·3°	48–79°				
Laboratory	May	65·0°	56–76°	20	20 (24–35 „)	0	*
	June	64·2°	50–82°	23	23 (28–43 „)	0	
	July	64·7°	52–77°	2	2 (20–22 „)	0	
	August	68·2°	53–83°	39	6 (23–35 „)	—	33 after 90–120 days
	September	64·5°	44–82°				

The influence of the temperature on the pupation period was investigated in the following experiments. Mr Bacot exposed pupae and mature larvae to low temperatures in the cool and cold rooms at the Lister Institute at Chelsea during August. The pupae were chilled by exposure for one week to a temperature of 54° F. (50–59°), followed by a week at 31·5° (28–35°); they were then kept in the laboratory for three weeks, and finally returned to the greenhouse. The mature larvae were exposed for a fortnight at 54° F., but not to a freezing temperature, and they pupated during this time. They were then returned to the laboratory and greenhouse with the other chilled pupae. Control pupae and larvae had been kept continuously in the tomato house.

One of those chilled had pupated the last week in April, and the moth emerged five days after its return to the greenhouse. The pupation period was 141 days, midway between the limits of the emergences of the controls (102–200 days), so no effect from the chilling is apparent in this case.

Twelve pupae which had pupated at the end of July and the beginning of August were chilled, and three moths emerged from these

after their return to the tomato house, with pupation periods of 38–40 days. Six out of the 12 control pupae produced moths with pupation periods of 20–32 days. In this case the chilling prolonged by about a week the short pupation period of those which have emerged, and apparently increased the tendency of the others to delay their emergence, nine of those chilled, as against six of those unchilled, being still pupae after 100 days.

The three mature larvae which pupated in the cool room have not emerged after 110 days, while in the control series of eight pupae obtained from the same batch of larvae, three emerged after 17–23 days, and five remain in the pupal stage. The chilling in this case seems to have prevented the early emergence of any of the moths.

In another experiment 30 pupae which had pupated August 1–5 were divided into three lots of ten each and placed on moist earth in the usual jars. One of these was put into a cucumber house, one into a tomato house, and the third out of doors under a wooden box covered by a folded heavy sack. The temperatures are given for the first month following the pupation. That in the cucumber house was 70·4° (Range 59–104°), and of the ten pupae eight emerged after periods of 18–22 days, one died, and one is still a pupa, after 120 days. In the tomato house the temperature was 71·3° (Range 52–94°), and four pupae emerged after 20–25 days, six still remaining in the pupal state. The temperature to which those outside were exposed was 66·9° (Range 42–97°), and one only emerged after a period of about 24 days, and the rest are still pupae. The influence of the temperature was thus very marked, but the tendency to prolong pupation was not abolished even by the relatively hot conditions of the cucumber house.

Some moths thus emerged in less than 50 days, and some after more than 100 days, but there were no emergences between these limits. At the end of April the glasshouses in this district were covered by snow for two days, and the consequent chill probably accounts for the long pupation periods of those insects which were nearly mature larvae at that time. The tendency to prolong pupation reappeared in the middle of a warm summer and became more intensified as the year went on. Those responding to it correspond to those individuals of the first brood in nature which do not emerge to form part of the autumn flight of moths, but remain as pupae from the end of one summer to the beginning of the next. Each pupa has thus an inherent tendency either to emerge quickly or to hibernate. The experiments show that an artificial raising of the temperature may reduce the tendency to

hibernation, but fails to abolish it in all within the limits tested. An artificial cooling may intensify it, or even make it total. The susceptible period in the insect's life is in the late larval and early pupal condition.

At the commencement of this work, judging by what was known at that time, it appeared that it might be possible to force all to emerge from the pupae by keeping up the temperatures of the greenhouses at the end of the growing season when there is no food for the larvae in the houses, and that the moths could then be destroyed by fumigating. The foregoing facts show that this is impracticable as the pupae would resist forcing at any temperatures to which the tomato houses could be raised.

[The following note completes the history of the pupae kept under observation through the winter in a greenhouse continuously heated. No moths emerged from September 5 to December 10, and very few in the latter month and in January. There was little relation between the dates of pupation and the dates of emergence of the moths. The longest pupation period was about 300 days (August to May). Those which had not emerged by the end of May were found to be dead.

No. of moths which emerged in	Mean Temp.	Pupated in July	August	September
December	60·6°	1	1	0
January	62·9°	1	3	4
February	63·2°	0	34	49
March	66·3°	3	34	74
April	66·8°	0	6	50
May	74·7°	0	2	15]

3. THE INFESTATION.

In captivity the shortest entire life cycle from moth to moth, when the larva was fed on tomato foliage, was 55 days. The eggs were laid on July 4; hatched on July 11 (7 days); larva matured and burrowed on August 6 (27 days); pupated August 8 (2 days); moth emerged August 27 (19 days). The mean temperature during this time was 72° F. (Range 52–94°). The life cycle under natural conditions in the tomato houses occupied rather longer on the average.

The life history of the insect was studied by the systematic examination of the 1600 plants in a 200-foot house from the end of April to the middle of September. This house was heated up in January and used for propagating one lot of plants in the early part of the year. It was planted out the second week in April. For the purposes of this experiment it was isolated from the rest of the block by a stretch of hessian

dropped from the gutter and fastened to a board running along the ground, the flight of moths to the rest of the block being thus prevented. The plants were not sprayed.

The plants were examined at intervals of three or four days. When they were small the examinations were made leaf by leaf, but when this became impracticable it was made plant by plant, attention being drawn to the presence of larvae by marks of recent feeding or by fresh droppings. All found were removed. Eggs, and larvae up to a week old, were counted as batches, and scattered larvae were counted indi-

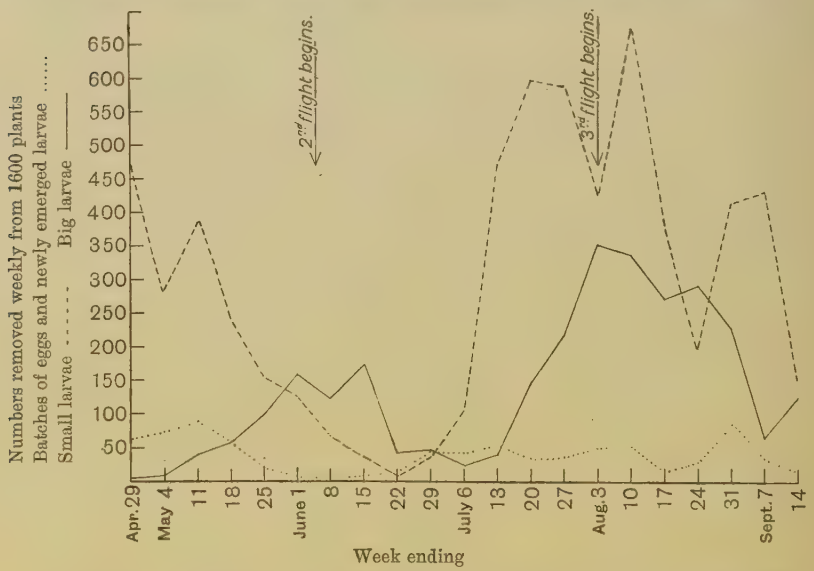

Diagram III. Showing the rise and fall in the numbers of larvae in the successive generations.

vidually and classified into two groups: (1) as "young" larvae, up to an age of about three weeks, and (2) as "old" larvae, which had passed the fourth moult. The numbers collected weekly in the two collections were plotted in a diagrammatic manner, the eggs being included with the newly emerged larvae in the week following their collection.

Diagram III thus shows the history of the pest over a period of four months, the numbers of larvae being of course much reduced by hand-picking. The dotted line represents the newly emerged larvae, the broken line the young larvae, and the continuous line the ones which

were nearly mature. The numbers of the newly-emerged fell to a minimum about June 8, and then again increased, and a similar fall and rise occurred about August 17. These dates represent approximately the beginning of the second and third broods of larvae of the year respectively. The numbers of old larvae fell to minima about July 6 and September 7, and this indicates that the first and second broods ended about these dates. As the infestation was getting out of hand in August moth trapping was resorted to in the house, and 174 moths were caught in this month, the numbers of larvae being much reduced at the end of the month in consequence. It has been known that there are two broods of larvae annually in the houses, since the reduction in numbers between these, as represented in the diagram at the end of June, is very noticeable to the observant grower. It has been a disputed point whether there is a third brood, but a study of the diagram shows that there is no doubt about this, at any rate in a favourable year. When the mature larvae fall to a minimum at the beginning of September the growing larvae of the third brood are very numerous and the demarcation between the broods is thus obscured.

The moths commence to emerge during February in houses heated up in January, as in the house under consideration. The emergence of the first flight continues to the end of May, and possibly later, being at a maximum about the beginning of this month. The reasons why this flight is so prolonged are: (1) the pupae do not respond equally to favourable temperatures; (2) they are in very different situations in the houses, some being close to the pipes, and some almost at the temperature of the outside air.

The moths of the second flight began to emerge from pupae bred from the first brood of larvae on June 4, while moths which were the offspring of these commenced to emerge the first week in August, the exact date being obscured by the slight overlapping of the second flight. Probably all the pupae which survive the winter produce moths which take part in the first flight. The very large majority of the offspring of these form the second flight, only a few delaying emergence, and probably none in a uniformly warm spring. About a quarter of the offspring of the second flight took part in the third flight in the present year, while the remaining three-quarters delayed emergence. In a cold year the second flight of moths might be so late that none of their offspring would emerge to form a third generation.

4. ORIGIN AND METHOD OF DISPERSAL.

There are three ways in which the pest may be introduced. Firstly, seedlings carrying the eggs or young larvae may be purchased from an infested nursery. Secondly, market baskets may bring in the pupae. Cases of both these are known, and they are sufficient to account for its appearance in new localities, supposing that it originated in only one place. Thirdly, the moth itself may enter through broken panes or open ventilators.

An experiment was carried out to discover to what extent this moth does enter the greenhouses. A block of seven 200-foot houses which had been used for propagating two lots of seedlings, was finally planted out the first week in May. The two houses at the east end of the block were isolated from the others by means of a sheet of hessian, and were made moth proof. Porches of hessian, with tightly fitting second doors, were built over the entrances at one end, while the doors at the other end were nailed up and caulked. The building was overhauled and put in perfect repair. The roof ventilators were screened with tinned steel woven wire, the mesh of which was one-sixth of an inch square. The large ventilators over the doors were replaced by cones of the wire mesh, which were directed downwards into the houses, and ended in sleeves of calico to which were attached glass jars half filled with water. In screening the roof ventilators it was necessary to arrange the wire in the form of bags in which the gear could work freely. In one of the houses these bags were completely closed, and in the other, one end of each opened into a calico sleeve which dropped into the interior of the house and opened into a glass jar of water. The sleeves were 18 ins. long, 6 ins. in diameter at the top, and 3 ins. at the bottom. This arrangement was devised under the impression, then generally held, that the moths invaded the houses in large numbers. The writer was informed that sometimes four or five were found jammed in the cracks around a door and agreed with the natural conclusion that they were trying to force their way in. The jars were arranged to trap moths deliberately trying to enter the houses, as it was thought that in trying to reach the plants below they would pass down the sleeves and be caught in the water. It is now known that the moths caught in the cracks were endeavouring to force their way out, and the experiment from this point of view was badly devised. The screening was not completed till June 14 owing to the difficulty of obtaining material (see Pl. IX, fig. 3).

A female *H. oleracea* was found in one of the jar traps on July 30,

and a dead male inside one of the screens on August 20. On the latter date 16 of the jars were replaced by shallow dishes, 4 ins. in diameter, filled with tanglefoot. These were placed at the tops of the calico sleeves which were tied below to keep them in position. At the end of September these traps were examined and four moths were found in them, three being *H. oleracea*, two females and one male, and the other a common Noctuid, *Mamestra brassicae*. It was thus proved that moths do pass into the houses in infested nurseries, though the method failed to give any estimate of the numbers of the invaders. The comparison of the infestations of the screened and the unscreened parts of the block confirmed this. It was not possible to destroy entirely the first brood of larvae, and some infestation was expected in all the houses from the offspring of these. Very few larvae were found until July 25, when in the two screened houses four mature ones were seen, and in two houses in the unscreened part, four batches of newly-emerged and seven older ones were found. On August 26 and September 10 an examination of the two screened houses gave 12 batches of newly emerged larvae and 164 older ones, and at about the same time on an equal number of plants in the unscreened part there were found 22 batches of newly-emerged and 689 older ones. Judging by these figures there were in August more moths to the house in the unscreened than in the screened part.

Table V. *Showing that the pest is a spreading one in the Lea Valley.*

Area	No. of Reports received	Average No. of years since tomatoes were first grown under glass	Average No. of years since the pest was first seen	Average No. of years since it became serious
Enfield Highway	7	19	14	12
Freezywater	3	16	11	10
Waltham Cross	6	17	11	7
Cheshunt	8	11	7	4
Flamstead End	6	17	4	2
Broxbourne	2	21	8	5
Hoddesdon	4	14	7	2
Ware	2	16	6	1
Waltham Abbey	5	12	9	5
Sewardstone	5	11	6	3

If it were a normal habit of this common moth deliberately to enter glasshouses and to breed upon tomatoes all the nurseries should have become infested soon after their institution, since it is very generally distributed. The history of the pest in the Lea Valley shows that this has not been the case. The growers have been questioned on the origin of the pest in their particular nurseries and the answers received are

summarised in Table V. In the first column the Lea Valley is divided up into areas, and the second gives the number of definite replies received from these. The remaining columns show the average number of years since: (1) tomatoes were first grown under glass; (2) the caterpillar was first seen in the houses; (3) it became a serious pest.

There is no gradation in the numbers in the third column, the industry having been established a considerable number of years throughout the district. The numbers in the last two columns show a distinct gradation, which bears a close relation to the relative positions of the areas. The earliest records are at Enfield Highway. From here it seems to have spread rapidly through the congested area of nurseries which follows the main road through Freezywater to Waltham Cross. The first records from the other localities are: Cheshunt 1908, Broxbourne before 1911 (indefinite), Hoddesdon 1909, Ware 1914. In the more outlying districts the earliest records are: Waltham Abbey 1906, Sewardstone 1911, Chingford 1913: and to the west of Cheshunt, in the Hammond Street and Flamstead End district, 1914.

It has therefore spread like an epidemic disease. Where the nurseries are congested it has moved rapidly, and where there is a gap it has lingered. In places it has made sudden jumps, for which the basket method of spread would account.

The moths which commence the infestation in each nursery are thus derived in some way from another nursery in which the pest is already established. In congested areas it may be that they are the actual moths which have escaped from infested houses, or they may be the offspring of such. The efforts of the insects to escape are so persistent that it is certain that a large proportion of those that emerge in the houses must succeed in doing so. These will naturally breed on suitable vegetation around the nursery, and as they are passing out in April and May, before the moth normally flies in nature, there is ample time for them to have a large or total second generation in the late summer of a favourable year. In the immediate neighbourhood an increase of the species will result from this which will readily encroach on adjoining nurseries. Several species of common butterflies and moths frequently blunder into the greenhouses and may be seen beating against the panes in their efforts to escape again. The more plentiful the species becomes the more likely are individuals to blunder in, and if it becomes excessively common the entry of a few each year becomes a certainty, since the total area of the ventilator openings is large. The escaping moths would thus account for the increase and the consequent spread.

This explanation of the spread of the pest, though difficult to prove conclusively, seems to be the most reasonable one, since it presupposes no modification of the instincts of the moth which cause it deliberately to invade places which it apparently dislikes, and to lay its eggs on foliage to which many of its larvae are unsuited.

The species outside is checked normally by a variety of factors: unfavourable weather; severe winters; the ravages of bats, birds, shrews, moles, toads and other animals; the attacks of hymenopterous and dipterous parasites. In the houses the climatic conditions are equable from early spring to late autumn, and the pupae are protected from the severity of the winter. Enemies are relatively few, the only important ones being spiders, the carnivorous beetle, *Carabus granulatus* L. and the ichneumon parasite, *Pimpla instigator* Fabr. The last of these, though of great benefit, loses much of its importance since it fails to keep pace with the rapid generations of the moth. These unnatural conditions foster those larvae which find tomato foliage a suitable diet, and this, together with the fact that the moth is a very prolific one, has enabled it to become a very serious pest in circumstances which are otherwise against it.

The moth is therefore not a normal pest of tomatoes and is much less firmly established in the houses than it at first sight appears to be. There is a danger that it will become a normal pest unless it is stamped out while it is still in some respects weak. If the methods adopted to control it are merely sufficient to bring its ravages within small dimensions its disappearance is not to be expected, and the cost of this partial checking must be regarded as a perpetual annual tax on the tomato industry.

5. CONTROL.

The instructions which follow have been framed with a view to the complete abolition of the pest, by attacking it in all its stages in the houses, and by preventing the escape of the moths to the outside, as far as this is reasonably possible, so that conditions around the nurseries may again become normal. If all the growers will carry out these instructions for a few years it is believed that the pest will cease to exist among them, but since the infection spreads in congested areas, the neglect of one will neutralise the efforts of the others from this point of view.

In order to effect this it is necessary that: (i) the larvae should be destroyed by spraying; (ii) larvae which appear when spraying is not

practicable should be trapped; (iii) the moths should be trapped throughout the season; (iv) pupae should be destroyed; (v) certain unnecessary conditions favourable to the insect should be avoided. These will be discussed in turn.

(i) Spraying.

Substances which are stomach poisons to the larvae should be used for this. They remain effective for a long time on plants protected from the rain, and are more certain than contact poisons. Suspensions of arsenate of lead paste, with a composition covered by a guarantee from the makers, should be used on young plants. It does not harm the foliage or prevent the setting of the fruit, and is a very stable substance. Paris green, though an effective poison for the larvae, is liable to damage the plants. Vegetable poisons, such as hellebore and nicotine, are costly for wholesale spraying. The sample of lead arsenate paste used in these experiments was guaranteed by the makers to contain 20 per cent. of arsenic pentoxide (As_2O_5).

As the arsenate is very heavy it sinks rapidly out of suspension unless very thoroughly agitated. It is liable to leave the machine at the correct strength at first. After a few rows have been sprayed it becomes too weak to be effective. Finally when the machine is nearly empty it becomes wastefully strong. The only kind of agitation that is quite efficient is constant shaking, and as this is difficult when the spray is being applied, some substance should be added to the water which will hold the substance up throughout the operation. A convenient and effective material to use is saponin, and it is economical as very little is necessary. It should be added to the water at the rate of 2 ounces in 100 gallons, or a small half-teaspoonful in 2 gallons. The paste should be mixed with a little of this solution and the thin cream obtained should be added to the bulk. Little agitation is then necessary to keep the suspension even until the machine is empty, and the spray will run in an even film which completely covers the foliage.

As an alternative to saponin the following spreader could be used. Slake 2 ounces of calcium oxide and suspend it in half-a-pint of water: work one ounce of casein into a cream and suspend it in a second half-a-pint of water: add one-third of this mixture to each 2 gallons of spray. This is approximately one pound of casein to 100 gallons of water. The spreader has been tested on a large scale at the rate of $\frac{1}{2}$, 1 and 2 lbs. of casein respectively to 100 gallons. The second concentration is an effective spreader but it is more costly in use than saponin at present

prices and is more trouble to mix. It should therefore not be used when saponin can be obtained.

Table VI. *Comparing the death date of the larvae on tomato plants sprayed with suspensions of lead arsenate paste* (20 *per cent.* As_2O_5) *of various strengths.*

Lbs. per 100 gals.		2	3	4	5	6	10
No. of larvae used		52	115	156	165	176	77
No. of larvae which pupated ...		18	2	7	4	4	2
Percentages surviving on succeeding days	1	97·1	94·6	90·2	82·9	84·7	85·3
	2	82·4	67·2	71·5	47·2	49·3	54·6
	3	61·8	46·0	37·3	19·3	28·4	22·6
	4	47·1	19·5	20·6	8·4	12·1	11·9
	5	35·4	13·3	8·5	6·6	5·8	3·9
	6	29·5	9·8	5·2	4·8	2·3	2·6
	7	26·6	7·1	3·9	3·6	1·7	0
	8	17·7	3·6	1·9	3·0	·6	—
	9	14·8	3·6	·6	2·4	0	—
	10	11·9	1·8	0	1·2	—	—
	11	6·0	·9	—	0	—	—
	12	6·0	·9	—	—	—	—
	13	3·1	0	—	—	—	—
	14	0	—	—	—	—	—

The larvae die off gradually when the lead arsenate is used at a strength of 2 lbs. to 100 gallons, or stronger. Some are found dead the day after the spraying but others survive a week or more. This is probably because they find the poison distasteful and the majority cease feeding before they have taken a fatal dose. After a time hunger forces them to recommence feeding, until finally a fatal dose is taken. In order to discover what concentration should be employed, small bushy plants in pots were sprayed with various strengths, from 2 to 10 lbs. of the paste to 100 gallons. When the spray was dry the plants were infested with a large number of larvae collected in the tomato houses. Half grown to mature ones were employed and they were kept from wandering either by enclosing the plants in muslin sleeves, or by placing them in large vessels covered with cloth. They were examined daily and the dead larvae were counted and removed. In each case a few of the larvae pupated but the varying numbers of these have little significance, as they were probably fully fed when placed on the sprayed plants. Two tests were made for each strength from 3 to 6 lbs. to 100 gallons and one test at strengths of 2 and 10 lbs. respectively. The results are given in Table VI, which shows under each strength the number of larvae employed and the percentages of these which survived

the succeeding days. If these numbers are traced down the columns and compared day by day it will be seen that there is a considerable advantage in using the substance at a greater strength than 3 lbs. to 100 gallons, while between 5 and 10 lbs. there is probably no more variation than could be accounted for by experimental error. However as the plants were considerably damaged by the feeding when the weaker concentrations were used, and at strengths of 6 and 10 lbs. only traces of feeding were seen, it is recommended that a concentration of 6 lbs. of the paste in 100 gallons should be employed. There is no advantage in using it at a greater strength.

A knapsack sprayer is quite efficient if saponin is used, and it was found that a man using one of these machines could easily keep pace with the planting over 25 acres of plants. The spray should fall downwards onto the foliage, and the operator should wear a piece of muslin over the face to prevent the poison getting into the eyes and nose. The plants should not be watered until the following day when the spray is thoroughly dry.

If larvae are seen feeding in the propagating houses the plants should be sprayed at once. In the houses known to be infested they should always be sprayed shortly after planting out. Another spraying should be carried out about a month before fruit picking will commence. This is the most important application and should be done in every block in the nursery where there has been any caterpillar in the previous year. It is a mistake to delay this final spraying because no larvae are seen feeding, as the arsenate cannot be employed on older plants without prejudice to the industry, and they may appear for the first time after it is too late. The grower will then be left with no remedy except picking off the insects by hand. This spray not only kills the larvae present when it is applied, but also all that subsequently feed on foliage that has been efficiently treated.

As some of the growers have been reluctant to adopt spraying, it seemed desirable to obtain practical proofs of this method of control over hand-picking. Reference was made above to a 200-foot house (one-tenth of an acre) which was isolated from the rest of the block by a stretch of hessian dropped from the gutter to prevent the passage of moths. The 1600 plants were untreated while those in the remainder of the block were sprayed twice with arsenate of lead. Each of the unsprayed plants was examined twice weekly and all larvae found were counted and destroyed. From four to six hours a week were devoted to this work—almost the equivalent of the entire time of one man over

an acre of plants. The work was therefore more thoroughly done than would be possible in a trade nursery. In spite of this, very poor control was kept, as only a small proportion of the larvae present were discovered at any one examination. Many matured and pupated, so that the summer brood was as large as the spring one. Much fruit was bitten and many stems were eaten through. The adjoining house was first examined on May 1, a fortnight after the plants were put out, and 79 larvae were counted to each hundred plants. These were not removed and a few days later the house was sprayed with arsenate of lead, the operation occupying one hour, and 10 gallons of diluted spray being used. Two days later it was again examined and 26 larvae were counted

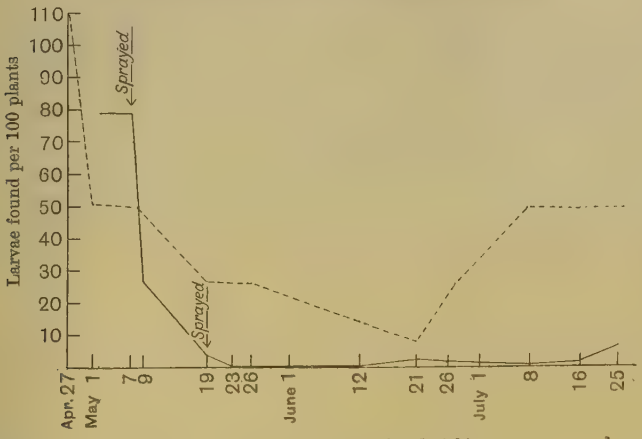

Diagram IV. Contrasting the control effected by hand-picking -------- and spraying with arsenate of lead ———.

to each hundred plants. Ten days after this another count gave four larvae to the hundred plants. It then received its second spraying as before and no more larvae were seen until June 21, and from that time on, till the comparison was stopped at the end of July, very few were seen, though later in the season they became more numerous.

Diagram IV shows the results of this experiment in a graphical manner. The continuous line represents the number of larvae found to the 100 sprayed plants in each of the 10 examinations made. The dotted line shows the number removed from each 100 plants in the unsprayed house on approximately the same dates. The hand-picking during these three months occupied over 70 hours and was inefficient. The spraying

cost an insignificant sum, occupied two hours to each house, and secured effective control for half the growing season.

This block was heated up in January and used for propagating. Consequently it was planted late and it was possible to give it the second spraying well on in May. When plants are put out in March to give early fruit at the beginning of June the second spraying could not be done after the end of April. As the blocks which receive these plants are usually unheated till the beginning of March, the first moths are later than in the case just considered. They will therefore be still emerging in numbers when there is much new unprotected growth on the plants, and the control will be less thorough than that described. This explains why those growers who have used the arsenate have found that, in spite of it, a few larvae are seen fully fed at the end of June. The offspring of these, and possibly of a few moths that have entered from outside, cause a heavy infestation in August and September, though less heavy than where spraying is not practised. It is therefore necessary to employ additional means of control.

Experiments were made with tuba root (*Derris*), a quantity of which was obtained by Mr Fryer, Entomologist to the Board of Agriculture. The specimens tested were prepared by Mr Tattersfield of the Rothamsted Experimental Station. In ordinary use this substance is said to be not poisonous to man and it could be used on plants in any stage. It was tested in several ways: (1) as a dry dust, alone and in dilution with powdered earth; (2) with saponin in watery suspensions, at various strengths from ·25 per cent. to 10 per cent. by weight of the powdered root, mixed and strained through muslin; (3) with saponin in watery suspensions of an alcoholic extract (six times the strength of the powdered root) at various strengths from ·08 per cent. to 2 per cent. by weight.

Tomato plants in pots were dusted or sprayed with these and infested with larvae collected in the nurseries. The dusting was unsatisfactory as it made the plants dirty and encouraged the growth of moulds. It need not be discussed further. The watery suspensions of the powdered root killed the larvae at a 10 per cent. strength, but a 5 per cent. strength failed to do so within a reasonable time. These strong mixtures also dirtied the foliage. Suspensions of the alcoholic extract proved very satisfactory sprays on an experimental scale. A series of 18 experiments showed that one part of this substance by weight in a thousand parts of water is a sufficiently potent spray. A plant sprayed with this was infested with 12 half-grown larvae which were confined to one leaf by means of a sleeve. Two days later seven of these were dead, and eight days after

they were put on they were all dead. Ten more half-grown larvae were then placed on another leaf, and ten days later these were all dead. The spray therefore remained potent for 20 days. The foliage of the plant was not damaged and the fruit set normally. This plant at the end of the experiment was photographed with a control plant of the same age which, without spraying, was infested with 10 half-grown larvae at the time the second lot were released on the sprayed plant. They completely ate a leaf each day and had destroyed the plant by the time those on the protected one were all dead (see Pl. IX, fig. 4). Similar experiments were carried out with strengths of 5, $2\frac{1}{2}$, $1\frac{2}{3}$, $1\frac{1}{4}$ and $\frac{5}{8}$ lbs. of the alcoholic extract in 100 gallons of water respectively, and each plant was infested with 22 larvae as described above. The results varied little from those detailed, except that with the weakest strength the death-rate was somewhat slower. None of the plants were damaged and the substance therefore appears to be safe to use, but no large scale experiments were carried out. At present there are no supplies of this substance available in England. Should it become available in large quantities it will prove a very useful adjunct to the arsenate of lead for later spraying. When the foliage of the plants becomes dense however treatment becomes more difficult, and will prove less effective in consequence.

(ii) Larva Trapping.

When spraying is not practicable the infestation may be reduced by trapping the mature larvae by means of sacks. They travel considerable distances in seeking suitable places in which to pupate, and sacking proves very attractive to them. Sacks placed about the houses will therefore catch a surprising number. They should be loosely folded and placed on the pipes under the gutters, or on the lower wires and touching the woodwork. Naturally the more used the better, but four or five to a house will collect hundreds of pupae in a moderately infested block. A count of them in 11 sacks, distributed in three houses and left for three weeks in September, gave a total of 729, or 66 to a sack (see Pl. X, fig. 5).

It is a long and tedious business to remove the larvae and pupae from them by hand, and it will be found more economical and thorough to collect them in a barrow and to dip them for half-a-minute into a cauldron of boiling water, and then to shake them. This will kill all the pupae, and also the wireworm beetles and the vast swarms of wood-lice which also find sacking attractive. They should be collected and dipped every 21st day. If they are left longer moths may begin to emerge.

(iii) Moth Trapping.

The trapping of the moths is as essential as the spraying. It is important that the escape of the moths to the outside should be prevented as far as possible, as they are responsible for the spread of the pest to neighbouring nurseries, and their offspring may re-enter the houses when the plants are not protected by the spraying. Trapping will not entirely prevent this escape but it must reduce it greatly. Apart from this, immediate advantage follows. The moth is long lived and can lay ten batches of eggs. As many of them may be caught soon after they leave the pupae the laying of most, or in some cases all, of these can be prevented.

The moths show no reaction to any lights which have been tested (candle flames, oil and acetylene lamps) and it is therefore necessary to attract them by baits. These are best exposed in jars which are tolerably deep in proportion to the width, have a pronounced shoulder, and a mouth opening about 2 inches across. Glass fruit preserving jars were found to answer well, the dimensions being, depth 8 ins., diameter 3 ins., width of neck 2 ins.

A fermenting mixture of crushed ripe tomato, water and yeast, was first tested as a bait in the houses, and a few moths were caught by this means. Five jars containing this mixture were hung on the wires near the gutters, and five others, each containing about three ounces of a mixture of ale and treacle, were placed in contrasting positions on the other sides of the gutters. In two nights the latter caught 52 moths, while the tomato traps caught only seven. Three jars of the following baits were then prepared: (1) ale alone; (2) treacle, one part; water, two parts; (3) treacle, one part; ale, two parts. One jar of each of these was placed in each of three houses and exposed for a fortnight. The distance between the traps was 100 feet, and their positions were interchanged twice during the exposure to equalise the chance of each bait. The numbers of moths caught were as follows: ale alone, 14; treacle and water, 12; treacle and ale, 109. The last of these was thus proved to be a very effective bait and was used in all subsequent trappings, a good quality dark treacle (present retail price, 9*d.* a pound) and ordinary cheap ale being employed. Waste beer was used in one set of traps but was found to be less effective, as the débris floated and formed a platform on which the moths could rest to feed, and escape. Even with the mixture usually employed it was found that some of the moths escaped after feeding, as a few were caught by hand in the houses and were found to

be distended with the bait. As it is necessary to have a moth trap widely open to allow the insects to flutter in it is difficult to prevent their escape by mechanical means, and it was therefore decided to poison the mixture.

Laboratory tests were made with sodium fluoride, ¼–1 per cent.; sodium arsenite, 2 per cent.; and lead arsenate paste, 2 per cent.; each mixed with ale and treacle and soaked up in muslin. These were placed in moth cages which included growing tomato plants and newly emerged moths. In the laboratory (T. 64° F.) the moths died off slowly. For example in the case of 1 per cent. sodium fluoride the average life of 20 moths was 7·5 days (4–10 days). In the tomato house (T. 70° F.) with the same poison the average life was 2·5 days (1–5 days). The probable explanation of this difference is that at the higher temperature the moths drink more freely. Exposed to 2 per cent. sodium arsenite in the tomato house, five moths had an average life of 3·6 days (1–5 days). 2 per cent. lead arsenate paste was found to be ineffective in the laboratory, eight moths all surviving six days, when the experiment was stopped. This study of moth poisoning was not completed when the number of available moths became too small for its continuance. When sodium fluoride was tested in the laboratory very considerable numbers of eggs were laid by the moths after they had taken the poison, but these were scattered all over the foliage and cage in ones and twos, and not in the normal large batches. One of the jars containing the ale, treacle and sodium fluoride was placed in a moth cage in a tomato house, and 11 newly emerged moths were released in it. All were caught the first night and no eggs were laid. The experiment was repeated with five moths, and four were caught the first night, while the remaining one, a male, was found in the trap on the third day. The moths are thus caught before they have laid any eggs in many cases, and the majority trapped in the houses were fresh specimens which had obviously flown little. However as a few eggs might be laid in the intervals between escape and death, the escape should be prevented as far as possible. The poison prevents fermentation and retards the formation of a scum on the fluid, and the dead bodies should be removed occasionally so that they do not form a platform.

Sodium fluoride is not a perfect poison and further search for a more effective one will be made. It has the advantage that it is not at all dangerous in use, and its employment in the greenhouses will ensure the early death of any moths which feed and escape from the jars.

Wholesale moth trapping was carried out in a block of 12 200-foot

houses. The plants had not been sprayed and no organised hand-picking had been practised. The first brood of larvae was at its maximum about the last week in May, and the second about the third week in July. It was then the most heavily infested of the 12 blocks in the nursery. The foreman in charge thought that it would be necessary to put all the hands available at the work of hand picking the larvae in order to save the crop. Experimental trapping with various baits had been commenced in June on a small scale, and at the beginning of July three traps baited with ale and treacle were placed in each house, one at each end and one in the middle, suspended from the wires near the gutters. This system of trapping was continued to the end of the season, with the exception of a fortnight at the beginning of August when all but four of the jars were removed and replaced by 72 pieces of muslin soaked in the bait to which 1 per cent. sodium fluoride was added. This method was considered unsatisfactory as, though the initial outlay is less, the attention required by them is greater than in the case of the jars, and as shown above a poisoned moth may lay a few eggs. Also no dead moths could be found, and it was thought that the growers would have more confidence in a method, the results of which were evident. When the full quota of jars were replaced on August 14 the poison was added to the bait.

At first the moths were caught at the rate of 80 a night, and the numbers steadily decreased to the end of July when 8 a night were being captured. The third flight of moths commenced while the exposed baits were out, and were caught at the rate of 175 a night when jars were replaced, and the nightly catch declined till, from September 16 onwards, it only averaged 2. A total of 1057 were taken in the second flight, and 1968 in the third flight, while an unknown number were poisoned. Of these 3023 moths approximately 71 per cent. were females, many of them distended with eggs. In order to estimate the effects of this trapping counts of the large conspicuous larvae were made occasionally in one of the end houses, each examination occupying about two hours. On July 23, before the trapping could have affected the numbers of these, 351 were seen, and a week later 150 (reference to Diagram III will show that this reduction was quite abnormal and could not have been obtained by hand-picking). On August 11, 65 were found, and on September 10, 16 only. The larvae following on the large third flight of moths were therefore very few, though in neighbouring blocks where early spraying had been done, those of the third brood could be collected by the thousand in September.

It was thus proved, by methods quite applicable to trade conditions that moth trapping combined with poisoning, is a most useful method of control. The experiment by itself showed that the danger of drawing moths into the houses is negligible, but as there is a confirmed impression that this risk is serious the matter will be discussed a little further. The probable reason why this idea arose is that the growers had no conception of the very large numbers of moths which exist in the infested houses, and so, when they exposed baits, they could account for the numbers trapped in no way except by assuming that moths were being attracted in.

If *Hadena oleracea* was drawn into the houses other common species of moths, which are attracted to these baits, should enter also. Only five individuals, other than this species, were noticed in the traps, and two of these strange moths, *Tryphaena pronuba* and *Xylophasia polyodon*, have been seen in houses where baits were not exposed. One of the baited jars was placed in a tomato house in such a way that it communicated only with the outside, by means of a calico sleeve and wide wire mesh cone. Moths from outside alone could thus get into it (see Pl. X, fig. 6). It was exposed from June 20 to the end of the season, the bait being renewed monthly. Only one moth, a male *H. oleracea*, was taken in it. Finally, even if a few moths were drawn in, they would be trapped or poisoned.

In order to determine how many traps should be used the arrangement in a block of 200-foot houses was varied. In the end house 12 were placed, and in the adjoining houses in succession, 8, 6, 4, 3, 3. They were left for five nights, and after the removal of the moths, were placed in the remaining six houses of the block in the same succession, the end house again receiving 12. After five more nights the moths were again removed and counted. The total numbers caught were as follows:

Number of traps ...	12	8	6	4	3	3
Moths caught ...	47	35	42	22	20	36

The last set of traps communicated on one side with houses in which at this time there were none, and it should be noted that they took less than double the number of moths taken by the three in the next house which were surrounded by other traps. The houses were 22 feet wide, so that the traps would appear to have an effective range of less than 44 feet. Apart from this set of traps, which cannot be used for purposes of comparison, the sets of 12, 8 and 6 were distinctly more effective than the sets of 4 and 3, and the set of 6 had an effect intermediate between those of 12 and 8. In another experiment 3 and 6 traps were exposed

alternately in an isolated house for six nights. On the three nights when three were used eight moths were caught, and on three nights when six were exposed the catch was 16. The conclusion drawn from these experiments was that in order to obtain the best results with this bait, jars should be placed every 40 feet down the houses: that is six to each 200-foot house, one at each end, and four others evenly distributed.

The fluid in the jars evaporates slowly in the greenhouses, and the traps remain effective as long as it covers the bottom. In the work just described the depth of the fluid varied from an inch to an inch-and-a-half, and it was found necessary to renew it every third or fourth week. The only attention the traps require during the interval is the occasional removal of the dead moths. These should not be dropped in the houses where they would prove a counter-attraction to the traps, but should be collected in vessels and thrown outside. In mixing the material, one part of treacle by volume should be placed in a vessel with two parts of ale, the exact proportion not mattering, and the mixture should be poured rapidly backwards and forwards from this into another vessel until it runs smoothly. It should then be distributed into the jars and the sodium fluoride added separately to each, as it dissolves very slowly. The amount that can be picked up conveniently on a sixpence (about $\frac{1}{30}$th of an ounce) is required for three fluid ounces.

(iv) Destruction of Pupae.

The picking baskets, especially those lined with sacking, need attention when the season is over, as they harbour pupae. Seven lined baskets were placed in an infested block, and at the end of three weeks were found to contain 24 pupae behind the lining. The practice has been to store these baskets over the winter and to bring them into the houses without attention when the fruit picking begins. The moths then emerge from them and their offspring commence feeding on foliage no longer protected by the early spraying. These baskets should be dipped in boiling water. It was proved by experiment that two seconds immersion is sufficient to kill the pupae, while 30 seconds did not harm the baskets.

Special baskets should always be kept for picking, and those from the market should never be allowed in the houses until they have been treated as described. This applies not only to tomato growing but to all nursery work. There is little doubt but that "red spider," and possibly "white fly" also, may be introduced into a greenhouse with a market basket. Those used for picking should be painted or marked

in some characteristic manner so that they may be kept for this purpose alone. If a nurseryman consents to store a salesman's baskets in his glasshouses over the winter he should insist on their being first sterilised by heat.

The canes should be dipped for a few seconds in boiling water to kill any pupae that may be in them.

The houses should if possible be drenched with boiling water before the mulch is removed. Most of the pupae on the ground lie in, or just below, this and if it is taken away untreated some of them will become moths in the following summer. The mulch also contains many wireworms and should not be spread on the fields untreated for this reason also. If the soil is heavy and wet the pupae lie very superficially, but in light dry friable soil they may go to a greater depth. Whenever the soil comes close up to a pipe a spadeful should be dug out from below it and spread thinly over the mulch before the drenching. The grower should inspect his own infested houses and if he finds the pupae at a greater depth than an inch along the walls and around the piers, a spadeful of earth should be removed and spread before the boiling water is used. After this operation a number of pupae should be collected from a variety of positions on the ground and should be placed in a plant-pot on moist earth. After an interval of three or four weeks they should be broken open. If the contents are green and fresh they are still alive and the drenching has been inefficiently done. If the contents are brown and corrupt, or dry, the insects are dead. It is not possible to tell after the brief immersion in hot water whether the pupae are alive or dead unless they are kept some time. Boiling water will be found more effective than carbolic acid for this pest.

Fowls or pigs would scratch up and eat a large number of pupae, and may be allowed in the infested blocks with advantage during the winter.

All crevices and joints in the woodwork should be examined from the ground to the ridge. The old nests of spiders frequently conceal pupae behind them. They are also often found spun up in the angles between the glass and the wood, and are then somewhat inconspicuous. They are often hidden in the wooden ventilators in the walls, and as moths from these would emerge late in the spring, owing to their being kept cool, they should be especially looked for. The stonework should be pointed and lime-washed. It would be a good plan to pass the flame of a painter's blow-lamp into all crevices of the woodwork, especially about the gutter-boards.

(v) General Precautions.

In dealing with this, as with most other pests, it is of great importance that the nurseries should be kept orderly. Weeds should not be allowed to grow either inside or in the neighbourhood of the houses. One reason for this is that the caterpillar can mature so much more quickly upon some of these than on tomatoes. Also, when a man is spraying the plants he is very liable to miss the weeds. Those below the shelves in the propagating houses and stray seedlings should be especially looked for and removed. The border of weeds often allowed to grow around the bases of the walls outside should be constantly hoed up. Caterpillars can easily feed up on those and pass into the houses to pupate.

Fallen broken fruit should never be allowed to lie about in the houses. The moths cannot feed on unbroken fruit but do so eagerly when the skin is ruptured and they can get at the juice. Under experimental conditions moths fed on this diet lived twice as long and laid three times as many eggs as those which were given no food.

6. APPARATUS AND MATERIALS REQUIRED FOR CONTROL.

A spraying machine, knapsack or other type.

A small open boiler for dipping baskets and sacks (a galvanised iron sanitary bin will do well).

Outfit for hot water drenching.

For each acre of tomatoes:

Sixty jars for moth trapping.
Arsenate of lead paste, 20 lbs.
Saponin, 6 ounces.
Thick treacle, 30 lbs.
Ale, 48 pints, to be purchased as required.
Sodium fluoride, 1 lb.

SUMMARY.

H. oleracea is not a normal pest of tomatoes grown under glass, and where it has become established as such it is still in some respects ill adapted to a greenhouse life on a tomato diet. The larvae eat the fruit because many of them are unable to survive on the foliage alone. In spite of this weakness, it has become a serious pest because the species is a prolific one and, once having entered a greenhouse, it usually be-

comes a prisoner there. In a normal year there are two complete generations and a partial third, and the moths are present in the houses continuously from February to October.

Spraying the young plants with arsenate of lead largely controls the first brood of larvae, but not entirely, because moths of the first flight of the year are still emerging when it is not practicable to use a poisonous spray on the plants. The plants should be sprayed three times when the larvae appear early: (1) when the seedlings are in pots; (2) just after planting out; (3) about a month before fruit picking begins. The last operation is the most important and the two previous ones may be omitted if there are no signs of larvae feeding.

Systematic moth trapping must be done throughout the growing season, because it will reduce the numbers of moths which pass out of the houses, and these, or their offspring blunder into the same or neighbouring greenhouses; and also because it is the most effective form of control when spraying is not practicable, and will reduce the infestation to a very great extent. Sixty jars baited with ale, treacle and 1 per cent. sodium fluoride should be used to each acre of glass. The dead moths should be removed frequently, and the jars should be rebaited every third week.

Broken fruit must not be allowed to lie about in the houses as the moths feed on this and become more prolific.

Many full grown larvae may be trapped in sacks placed about the houses. The sacks should be collected and dipped in boiling water every third week.

Pupae should be destroyed in the winter.

Special baskets should be kept for fruit picking, and those from the markets should never be allowed in the houses.

The pest spreads rapidly through areas where the nurseries are congested owing to the escape of moths from the infested houses. It may be introduced into isolated localities by means of market baskets, or by plants purchased from infested nurseries. On its first appearance every method of control should be applied at once, as attempts to check it by picking off the larvae by hand in trade nurseries have almost invariably ended in failure.

DESCRIPTION OF PLATES

PLATE VIII.

Fig. 1. The damage done to tomato plants by the larvae of *Hadena oleracea*. The shoot is eaten through, the stem is bitten into, and a larva is eating a fruit.

Fig. 2. The larva of *H. oleracea* feeding on the pith of a tomato plant.

PLATE IX.

Fig. 3. Greenhouse screened against invasion by *H. oleracea*.

Fig. 4. Showing the benefits to be obtained by spraying. The plant on the left was sprayed with a suspension of an alcoholic extract of tuba root and then infested with 22 larvae which were all poisoned. The other plant was not sprayed and was infested with 10 larvae which destroyed it in a week.

PLATE X.

Fig. 5. A sack exposed for three weeks in a tomato house infested by *H. oleracea*, showing the trapped pupae.

Fig. 6. Showing a baited trap in a tomato house, communicating only with the outside. In three months only one *H. oleracea* was caught in it. In the same period over 3000 were captured in similar traps in a block of 12 infested tomato houses.

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 6.

A QUANTITATIVE ANALYSIS OF PLANT GROWTH.

PART I.

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(With 9 text-figures.)

PAGE

Introduction 103

Chapter I. The Relative Growth-Rate Curve for Maize 106

Average Growth-Rate 120

Summary 120

Introduction.

The quantitative analysis of plant growth is a branch of plant physiology to which adequate attention has not as yet been paid, but which should be able nevertheless to yield results of much theoretical interest and economic importance. Methods for obtaining data for the analysis of plant growth under ordinary cultural conditions are in general simple, consisting principally of periodic dry-weight and leaf-area measurements, and a quantity of excellent data of this nature has already been collected and exists in the literature. As yet a thorough analysis of these results has not been presented. Attempts have been made to fit in a few isolated results with various empirical laws without wide examination of existing data.

For example it has been recently suggested by V. H. Blackman(1) that the growth of an annual plant can be treated as a process following the compound interest law expressed by the formula

$$W = W_0 e^{rt},$$

where W = the dry-weight of the plant at time t, W_0 = the initial dry weight of the plant, r = the rate of interest or "efficiency index" of dry-weight production, and e = the base of the natural logarithms.

Another suggestion is that the growth of a plant is similar to an autocatalytic reaction, and that it can be expressed by the formula

$$\log \frac{x}{A - x} = K\,(t - t_1),$$

where A = the maximum dry-weight of the plant, x = the dry-weight of the plant at any time t, t_1 = the time at which the weight of the plant is half the final dry-weight, and K = a constant. This suggestion was put forward by Robertson (24 and 25) and has received the support of Reed and Holland (21) and of Rippel (22 and 23).

Finally Mitscherlich (14, 15 and 16) has attempted to apply to plant growth as measured by dry-weight increase the following formula

$$\log (\sqrt[n]{A} - \sqrt[n]{y}) = \log \sqrt[n]{A} - c\,.\,x.$$

In this formula n = a variable quantity indicating the probable number of environmental factors, A = the maximum possible dry-weight attainable by the plant in question, y = the dry-weight of the plant at time x, the time x being expressed in vegetation periods (Vegetationsabschnitten) of arbitrary length.

A fuller consideration and criticism of these suggestions will be given in subsequent chapters.

In the present paper the primary objective is to attempt to obtain a concrete idea of the growth and development of the plant. At the outset it will be best to confine our attention to simple cases and we propose to devote the first chapter to a consideration of an annual plant.

Certain data are required: periodic dry-weight measurements of the whole plant (and its various parts) at short intervals throughout its life, starting from the seed at the time of sowing; corresponding periodic leaf-area measurements; data with regard to light, temperature, and water supply. To avoid the error due to individual variation, a large number of plants should be used for each dry-weight measurement and where possible uniform 'pure-line' material should be employed.

There are various methods of presenting the results, and in the first instance we shall use the *relative growth-rate curve*. The principle of the proposed method of expressing rate of growth is analogous to that of the method by which the rate of most reactions, both chemical and physiological, are expressed, namely, amount of change per unit of material per unit of time. Since the amount of material in the growing plant is constantly changing, and since the relative rate of growth is not constant, as the following analysis will show, to achieve mathe-

matical accuracy the increase should be measured over an infinitely short period. This procedure is manifestly impossible, and as we have no exact knowledge of the way in which the relative rate of growth varies over a given period we have adopted the following purely conventional method of defining relative rate of growth. The relative rate of growth of a plant during any given week in its life-cycle is the amount

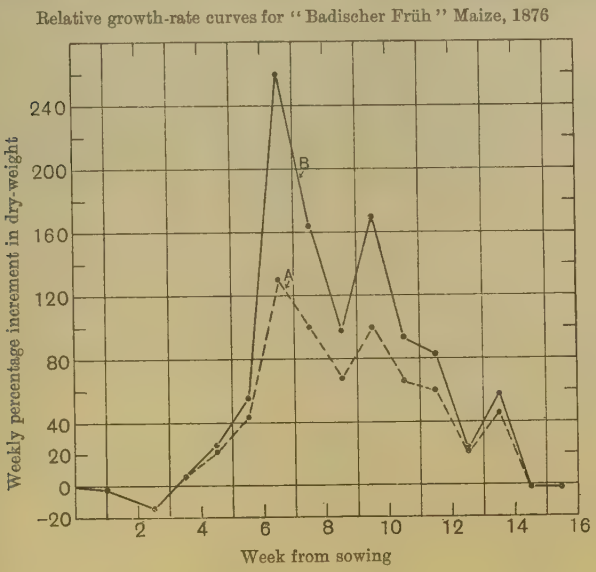


Fig. 1.

of dry matter which 100 g. of dry matter taken at the beginning of the week adds during the week. A week has been chosen since this is the usual interval between determinations of dry-weight in most experiments on growth in plants[1]. It must be realised that the method does not pretend to mathematical accuracy being merely an approximate average for the week, but with such results as are at present available nothing more accurate can be obtained. Even if measurements over

[1] When results are not given for a week we have calculated the increase per 100 g. for the period and divided the result by the number of weeks in the period: for example, if the period is 8 days and 40 g. increases by 20 g. during that period, then the relative rate is $\frac{20 \times 100}{40} \div \frac{8}{7}$.

shorter intervals were available, until we gain knowledge of a mathematical law according to which the rate changes, we cannot determine the rate at any given time.

It might be suggested that allowance could easily be made for the continuous increase in the dry-weight during the week by assuming that this takes place at a uniform rate, and consequently that by means of the following logarithmic formula the rate could be determined:

$$\log W - \log W_0 = r,$$

where W = the dry-weight at the end of the week, and W_0 = the dry-weight at the beginning of the week.

In curve A, Fig. 1, this allowance has been made. In Curve B the ordinates are relative growth-rates calculated by our method, that is, without making allowance for the continuous increase during the week. These curves show similar variations in relative rate from week to week. The more complicated method, however, does not achieve accuracy as it rests on the assumption that the rate remains constant during the week, an assumption manifestly incorrect since the rate varies from week to week. Both methods are purely conventional and only approximate to accuracy, and nothing definite is to be gained by adopting the more complicated procedure.

The relative rate of plant growth at any time may be taken as an expression of the efficiency of the plant at that time in producing dry matter. It must be remembered from what we have said above that the actual value of the figures for the growth-rate is only an average of the changing rate during a week. They are, however, valid for purposes of comparing the rate of a plant's growth from week to week.

The gist of the method described above of presenting the results of growth experiments has been previously briefly put forward by Kidd and West(9).

CHAPTER I.

THE RELATIVE GROWTH-RATE CURVE FOR MAIZE.

The most complete set of data for one plant is to be found in a series of papers published in Germany many years ago under the general direction of U. Kreusler(10, 11, and 13). From among the many results recorded, we have chosen those for maize, since the growth of this plant was studied in four successive years. The data include not only weekly dry-weight measurements and corresponding leaf-area measurements.

but also environmental conditions such as light, temperature, water-supply, etc. The dates of the first appearance of the flowers and of seed formation are also given. The work appears to have been carried out without any pre-conceived idea as to what the results would be, and the results themselves have not as yet been worked out nor have they received critical consideration although collected and published 40 years ago. These results will be analysed in this and in the following chapter, and certain interesting conclusions reached. We have constructed from Kreusler's data the tables and figures presented in this paper. Figs. 2 and 3 show respectively the relative growth-rate curves for "Badischer Früh" maize, the rates being calculated, as above described, on the basis of weekly periods for the years 1875–1878 inclusive, and for five different varieties of maize calculated on the same basis for the year 1875.

Table I.—"*Badischer Früh*" *Maize grown at Poppelsdorf in* 1875.

Date of harvest 1875	Growth period Days	Total dry weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Mean temperature °C.	Record of appearance of ♂ and ♀ flowers
11th May	.	0·206						
				(30)*				
1st June	21	0·268	0·062	10	33·3	124	14	
8th „	7	0·559	0·291	108	97·8	177	19·3	
15th „	7	1·069	0·510	91	181·1	170	17·1	
				(129)				
23rd „	8	2·448	1·379	113	405·1	167	16·6	
30th „	7	4·776	2·328	95	889	186	17·0	
7th July	7	11·077	6·301	132	1543	139	19·9	♂ flowers
				(113)				
13th „	6	23·619	12·542	132	2646	112	18·1	♀ flowers
				(85)				
21st „	8	43·844	20·225	74	3633	83	18·8	
				(28)				
27th „	6	55·934	12·090	33	3291	59	17·6	
3rd Aug.	7	72·875	16·941	30	3617	50	16·9	
10th „	7	76·619	3·744	5	3630	48·5	19·1	
17th „	7	84·332	7·713	10	2933	34·5	21·5	
24th „	7	89·621	5·289	6	2696	30	19·8	
31st „	7	100·380	10·759	12	2907	29	19·0	
7th Sept.	7	130·478	30·098	30	2986	23	16·1	
				(21)				
15th „	8	158·139	27·661	18	2335	14·8	17·5	

* The figures in brackets in column 5 give the percentage increase in dry-weight for the number of days stated in column 2.

Table II.—"*Badischer Früh*" *Maize grown at Poppelsdorf in* 1876.

Date of harvest 1876	Growth period Days	Total dry-weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Number of hours of sunshine	Mean temperature for the week °C.	Record of appearance of ♂ and ♀ flowers
11th May		0·3264							
				(−2·91)*					
24th „	13	0·3169	−0·0095	−1·57				9·8	
31st „	7	0·2724	−0·0445	−14	8·4	31	42	13	
7th June	7	0·2914	+0·0190	+ 7	19·0	65	61	15·1	
14th „	7	0·3642	0·0728	25	41·4	113	16	16·3	
21st „	7	0·5674	0·2032	56	92·0	162	57	16·9	
28th „	7	2·0733	1·5059	260	350·8	170	102	19	
5th July	7	5·655	3·582	164	987·0	172	42	17·6	
12th „	7	11·151	5·496	97	1794·5	159	45	20	
19th „	7	30·265	19·114	170	3272·6	108	71	17·6	♂ and ♀
26th „	7	58·609	28·344	93	4959·8	85	49	18·5	flowers
2nd Aug.	7	106·908	48·299	83	6196·7	58	93	20·3	
9th „	7	131·169	24·261	22·7	5530·7	42	76	18·3	
16th „	7	207·373	76·204	58·2	6666·7	32	94	21·9	
23rd „	7	204·436	−2·937	−1·42	6201·4	30·5	77	21·6	
30th „	7	202·168	−2·268	−1·12	4231·4	21	10	14·5	

* The figure in brackets in column 5 gives the percentage increase in dry-weight for 13 days.

Table III.—"*Badischer Früh*" *Maize grown at Poppelsdorf in* 1877.

Date of harvest 1877	Growth period Days	Total dry-weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Number of hours of sunshine	Mean temperature for the week °C.	Record of appearance of ♂ and ♀ flowers
17th May		0·3353							
				(−3·88)*					
29th „	12	0·3223	−0·013	− 1·9			14	11·9	
5th June	7	0·2819	−0·404	−12·6	5·43	19·2	44	16·6	
12th „	7	0·2877	+0·0058	+ 2·13	45·7	159	33	19·1	
19th „	7	0·9395	0·6518	227	168·8	180	54	18·7	
26th „	7	2·500	1·650	176	477·5	192	32	18·8	
3rd July	7	6·365	3·775	150	1060	166	40	18·0	
10th „	7	10·637	4·272	67	1671	157	20	14·7	
17th „	7	24·447	13·810	130	3216	132	27	19·0	♂ flowers
24th „	7	41·408	16·961	69	3788	92	38	17·5	♀ flowers
31st „	7	66·498	25·09	61	4591	69	20	18·6	
7th Aug.	7	88·654	22·156	33·4	4934	55·5	40	16·4	
14th „	7	119·842	31·188	35	5298	44	19	19·3	
21st „	7	135·532	15·690	13	4852	35·5	30	19·5	
28th „	7	140·782	5·250	3·9	4158	29·5	17	18·1	
4th Sept.	7	179·973	39·191	28	4332	23	25	16·6	
11th „	7	187·795	7·822	4·35	4035	21·5	17	13·0	
18th „	7	201·293	13·498	7·2			18	16·0	
25th „	7	220·709	19·416	9·4			9	9·7	
2nd Oct.	7	199·970	−20·739	−9·4			22	7·9	
9th „	7	204·017	+4·047	+2·0			9	9·0	

* The figure in brackets in column 5 gives the percentage increase in dry-weight for 12 days.

Table IV.—"*Badischer Früh*" *Maize grown at Poppelsdorf in* 1878.

Date of harvest 1878	Growth period Days	Total dry-weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf area to dry-weight Sq. cm. per gm.	Number of hours of sunshine	Mean temperature °C.	Record of appearance of ♂ and ♀ flowers
20th May		0·3282							
28th „	8	0·3280	−0·0002					12·4	
4th June	7	0·2870	−0·041	−12·5			40	13·6	
11th „	7	0·2550	−0·032	−11·2	17·9	70	27	15·5	
18th „	7	0·3080	+0·053	+20·8	29·2	95	19	15·1	
25th „	7	0·6370	0·329	106·5	124·4	195	40	17·9	
2nd July	7	2·319	1·682	264	419·2	181	36	19·8	
9th „	7	4·654	2·335	100	762·2	174	16	17·1	
16th „	7	9·019	4·365	94	1301	144	20	16·8	
23rd „	7	20·001	10·982	122	2136	107	57	19·6	♂ and ♀
30th „	7	34·557	14·556	72	2805	81	23	19·8	flowers
6th Aug.	7	57·587	23·030	66	3384	59	35	18·2	
13th „	7	70·095	12·058	21·7	3047	43·5	32	20·1	
20th „	7	85·165	15·070	21·4	3025	35·5	35	19·3	
27th „	7	111·649	26·484	31	2976	26·5	17	17·8	
3rd Sept.	7	124·760	13·111	11·7	2684	21·5	21	19·0	
10th „	7	121·990	−2·770	−2·2	2387	19·5	35	19·2	

Table V.—"*Hühner*" *Maize grown at Poppelsdorf in* 1875.

Date of harvest 1875	Growth period Days	Total dry-weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Mean temperature °C.	Record of appearance of ♂ and ♀ flowers
11th May		0·127						
				(17)*				
1st June	21	0·149	·022	5·7	28·9	194	14·0	
8th „	7	0·476	·327	220	86·3	181	19·3	
15th „	7	0·824	·348	73	153	186	17·1	
				(114)				
23rd „	8	1·765	·941	100	371	210	16·6	
30th „	7	2·847	1·082	61	627	220	17·0	
7th July	7	7·292	4·445	156	895	123	19·9	♂ and ♀
				(59)				flowers
13th „	6	11·570	4·278	69	749	65	18·1	
				(86)				
21st „	8	21·576	10·006	75	1416	66	18·8	
				(89)				
27th „	6	40·735	19·159	104	2126	52	17·6	
3rd Aug.	7	55·918	15·183	37	1917	34	16·9	
10th „	7	60·648	4·730	8·5	2196	36	19·1	
17th „	7	73·946	13·298	22	2254	31	21·5	
24th „	7	90·491	16·545	22	2090	23	19·8	
31st „	7	88·212	−2·279	−2·5	2032	23	19·0	
7th Sept.	7	81·618	−6·594	−7·5	1367	17	16·1	
				(−6·4)				
15th „	8	76·385	−5·233	−5·6	665	9	17·5	

* The figures in brackets in column 5 give the percentage increase in dry-weight for the number of days stated in column 2.

Table VI.—"*Oberländer*" *Maize grown at Poppelsdorf in* 1875.

Date of harvest 1875	Growth period Days	Total dry-weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Mean temperature °C.	Record of appearance of ♂ and ♀ flowers
11th May		0·107						
				(51)*				
1st June	21	0·162	0·055	17	31	192	14·0	
8th „	7	0·467	0·304	188	96·7	207	19·3	
15th „	7	0·955	0·488	105	165·3	173	17·1	
				(89)				
23rd „	8	1·839	0·884	78	374·1	203	16·6	
30th „	7	3·097	1·258	67	621·0	201	17·0	
7th July	7	6·758	3·661	118	668·6	99	19·9	♂ and ♀ flowers
				(114)				
13th „	6	14·448	7·690	133	950·6	66	18·1	
				(72)				
21st „	8	24·890	10·442	63	1098	44	18·8	
				(21)				
27th „	6	30·180	5·290	25	1407	47	17·6	
3rd Aug.	7	51·196	21·016	70	1653	32	16·9	
10th „	7	70·978	19·782	39	2217	31	19·1	
17th „	7	59·110	−11·868	−17	2359	40	21·5	
24th „	7	81·687	22·577	38	1464	18	19·8	
31st „	7	73·921	−7·766	−9	1235	16	19·0	
7th Sept.	7	74·120	0·199	0·3	1716	10	16·1	
				(18)				
15th „	8	87·192	13·072	15	514	6	17·5	

* The figures in brackets in column 5 give the percentage increase in dry-weight for the number of days stated in column 2.

Table VII.—"*Ungarischer Früh*" *Maize grown at Poppelsdorf in* 1875.

Date of harvest 1875	Growth period Days	Total dry-weight of a single plant Gm	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Mean temperature °C.	Record of appearance of ♂ and ♀ flowers
11th May		0·2696						
				(−0·88)*				
1st June	21	0·2672	−0·0024	−0·29	31·0	116	14·0	
8th „	7	0·609	0·342	128	118·9	196	19·3	
15th „	7	1·110	0·501	82	190·2	172	17·1	
				(93)				
23rd „	8	2·143	1·033	81	393·2	184	16·6	
30th „	7	4·123	1·980	93	807·0	196	17·0	
7th July	7	12·101	7·978	195	2109	174	19·9	♂ and ♀ flowers
				(92)				
13th „	6	23·244	11·143	107	3030	130	18·1	
				(91)				
21st „	8	44·48	21·236	80	4329	97	18·8	
27th „	6	70·46	25·98	65	5635	80	17·6	
3rd Aug.	7	104·98	34·52	49	8827	58	16·9	
10th „	7	92·85	−12·13	−12	4975	54	19·1	
17th „	7	121·78	28·93	30	4894	40	21·5	
24th „	7	169·53	47·75	38	3454	20	19·8	
31st „	7	212·72	43·19	25	4807	23	19·0	
7th Sept.	7	213·29	0·57	0·3	5204	24	16·1	
				(−5)				
15th „	8	202·19	−11·10	−4	2738	14	17·5	

* The figures in brackets in column 5 give the percentage increase in dry-weight for the number of days stated in column 2.

Table VIII.—"*Pferdezahn*" *Maize grown at Poppelsdorf in* 1875.

Date of harvest 1875	Growth period Days	Total dry-weight of a single plant Gm.	Increase in dry-weight since last harvest Gm.	Weekly percentage increase in dry-weight since last harvest	Leaf-area Sq. cm. per plant	Ratio of leaf-area to dry-weight Sq. cm. per gm.	Mean temperature °C.	Record of appearance of ♂ and ♀ flowers
11th May		0·294						
				(−3·4)*				
1st June	21	0·286	−0·010	−1·1	36·2	126	14·0	
8th „	7	0·517	0·232	80	77·9	150	19·3	
15th „	7	1·023	0·506	98	177	174	17·1	
				(74)				
23rd „	8	1·781	0·758	65	335	188	16·6	
30th „	7	3·826	2·045	115	730	190	17·0	
7th July	7	9·064	5·238	135	1686	187	19·9	
				(91)				
13th „	6	17·292	8·228	106	2578	149	18·1	
				(72)				
21st „	8	29·704	12·41	63	3984	134	18·8	
				(85)				
27th „	6	54·998	25·29	100	6274	114	17·6	
3rd Aug.	7	73·949	18·95	32	6622	90	16·9	
10th „	7	108·68	34·73	46	8453	77	19·1	♂ and ♀
17th „	7	153·61	45·93	41	8823	57	21·5	flowers
24th „	7	173·18	18·57	12	8258	48	19·8	
31st „	7	210·37	37·19	21	7090	34	19·0	
				(−16·5)				
7th Sept.	7	245·09	34·72	−14·5	9200	38	16·1	

* The figures in brackets in column 5 give the percentage increase in dry-weight for the number of days stated in column 2.

In forming a clear picture of the growth of the plant as presented by its increase in dry-weight, it is as well to keep in mind the fact that from 80 % to 90 % of the dry-weight is the result of the process known as carbon-assimilation and that the actual percentage of the dry-weight of the plant derived from the mineral constituents of the soil is relatively small (cf. Hornberger (6), Monnier (17), Rabinovitch (20) and others (26, 4, 8 & 3))[1].

[1] Jones and Huston(8) give the following figures for the ash of maize at different periods:

Date of sampling (week from sowing)	Ash (percentage of the total dry-weight of the plant)
3rd	12·0
9th	12·2
11th	8·7
14th	6·0
16th	5·3
18th	4·8
19th	4·1
20th	4·1

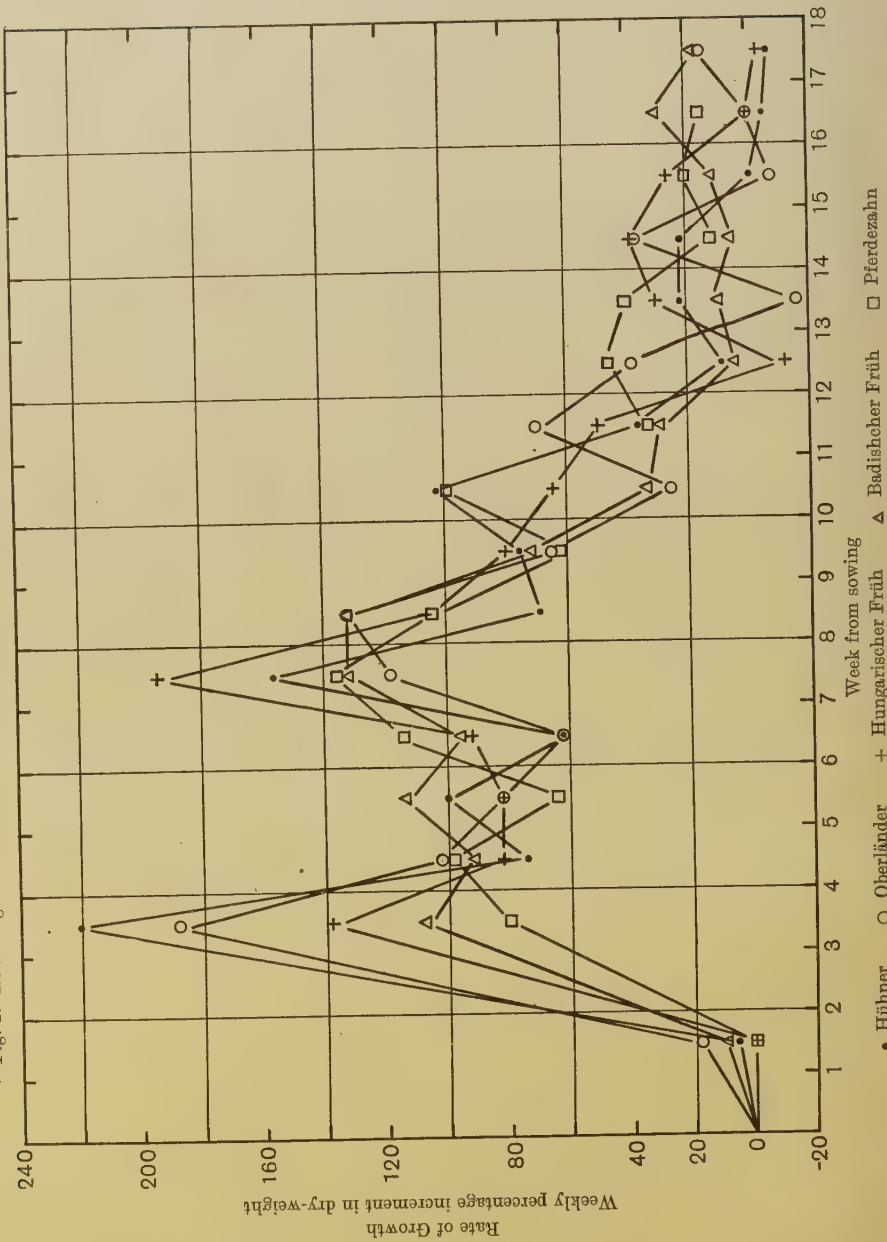


Fig. 2. Relative growth-rate curves for five varieties of maize grown at Poppelsdorf in the year 1875.

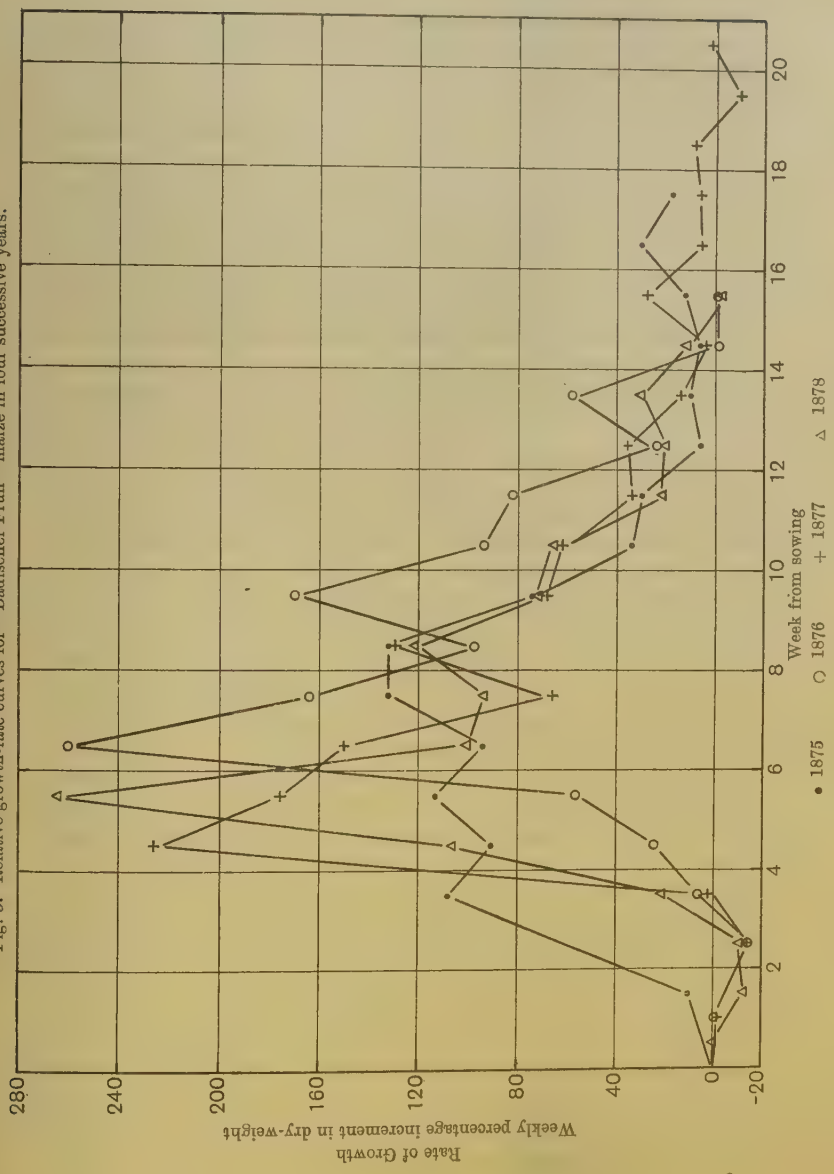


Fig. 3. Relative growth-rate curves for "Badischer Früh" maize in four successive years.

It follows that the relative rate of growth at any time is almost the same as the difference between the rates of assimilation and respiration per 100 g. dry-weight at that time.

We will now proceed to consider the curves. In following the curves in Fig. 3 from the date of sowing, there is seen to be an initial phase lasting for about three weeks during which the rate of growth is negative, in other words, the plant is actually losing in weight[1]. This phase of negative growth persists until a point in the development of the plant is reached at which approximately four leaves have appeared. During the time occupied by germination, before the appearance of these leaves, the negative rate of growth is clearly to be attributed to a loss of carbohydrate through respiration. The order of magnitude of the loss in dry-weight through respiration in germinating seeds is 3 % to 6 % of their dry-weight per day at 16° C. (Garreau (5)). In the latter part of the period, where, despite the fact that the plant possesses from 1–4 leaves, the negative rate of growth persists, it is obvious that any increase in dry-weight due to assimilation is more than counter-balanced by a loss in weight through respiration. Evidence obtained by an analysis of Kreusler's data as to whether the leaves at this stage perform their normal assimilatory function, or not, will be considered shortly. After this initial phase there ensues a short period varying from 1–4 weeks during which the rate of increase in dry-weight rises rapidly to its maximum value, followed by a long period constituting the remainder, and larger part, of the life-cycle of the plant, throughout which the rate of growth falls off more or less continuously. This falling part of the curve, however, shows subsidiary maxima.

The question arises of what kind of change in the plant this perfectly definite type of curve in the main period of growth is an expression. It is clear that this main rise and fall must be due to an increasing difference between the rate of assimilation and the rate of respiration per unit dry-weight in the first phase and to a decreasing difference in the second phase. The order of magnitude of respiration in terms of dry matter consumed per week during the main growth period of the plant is probably not greater than 20 %–40 %, which is the order of magnitude of the loss in dry-weight through respiration during germination. As against this the actual percentage increase in dry-weight per week varies from 0 % to over 200 %, this being the balance when loss due to respiration is

[1] In the year 1875 the first dry-weight measurement was not taken until the end of the third week. The average plotted in Fig. 3 gives no indication of the variations in the individual weekly growth-rates.

subtracted from gain due to assimilation, etc. Consequently it is obvious that changes in the rate of respiration per unit dry-weight of sufficient magnitude to affect the rate of growth to the extent observed are inconceivable. We must turn therefore to the changes in the rate of assimilation per unit dry-weight in order to account for the main rise and fall which characterises the growth-rate curve. Brief consideration will show that the rate of assimilation per unit dry-weight is most probably a function of the amount of leaf-area per unit dry-weight mainly, and it is interesting to enquire therefore to what extent changes in leaf-area per unit dry-weight correspond with those in the rate of growth. The values of the ratio of leaf-area to dry-weight throughout the life-cycle of the plant can be calculated from Kreusler's data, and when these values are plotted against time there appears a striking similarity between this curve and the growth-rate curve (see Figs. 4, 5, 6 and 7).

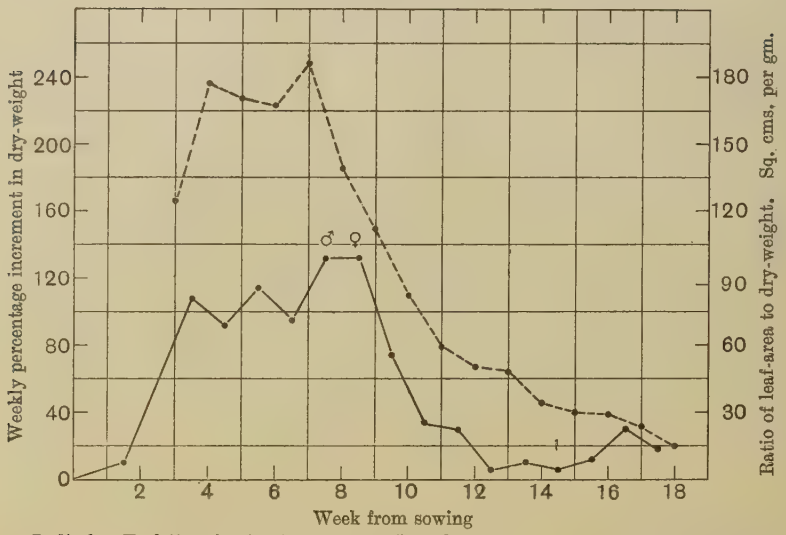
From this we may conclude, therefore, that the main rise and fall shown by the growth-rate curve is merely an expression of the rise and fall in the ratio of leaf-area to dry-weight.

To return to the question of the assimilation of the young leaves on their first appearance, an inspection of Figs. 4, 5, 6 and 7 will show that at this stage the ratio of the ordinate of the growth-rate to that of the leaf-area curve (which ratio is really a measure of the increase in dry-weight *per unit leaf-area*) is a negative or very small quantity compared with the ratio during the main period of high relative rate of growth. This fact strongly suggests that the assimilatory power of the young leaves for some time after their first appearance is negligibly small. It is interesting to find that this inference which is drawn from an analysis of plant growth, as presented in this paper, is corroborated by direct experimentation on the assimilatory power of young leaves (Irving(7) and Briggs(2))[1].

Another point of interest which arises from a comparison of the leaf-area ratio with the growth-rate curve is that, while the growth-rate curve exhibits one or more subsidiary maxima in the falling phase, the leaf-area ratio curve on the other hand falls uninterruptedly.

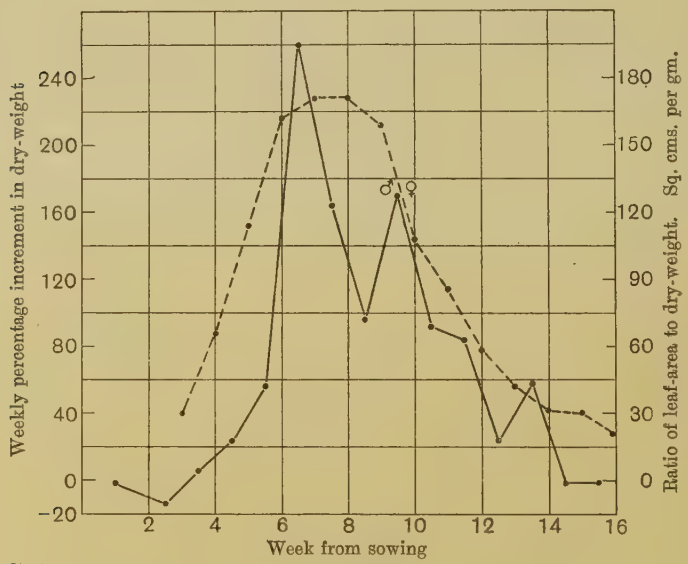
With regard to these subsidiary maxima exhibited by the growth-rate curve there is a significant correlation between the times of their occurrence and the recorded times of the first appearance of the male and female flowers (see Figs. 4–8). Results obtained with maize by Morgen(18) and Osswald(19) who worked in conjunction with Kreusler,

[1] Also unpublished results for maize.



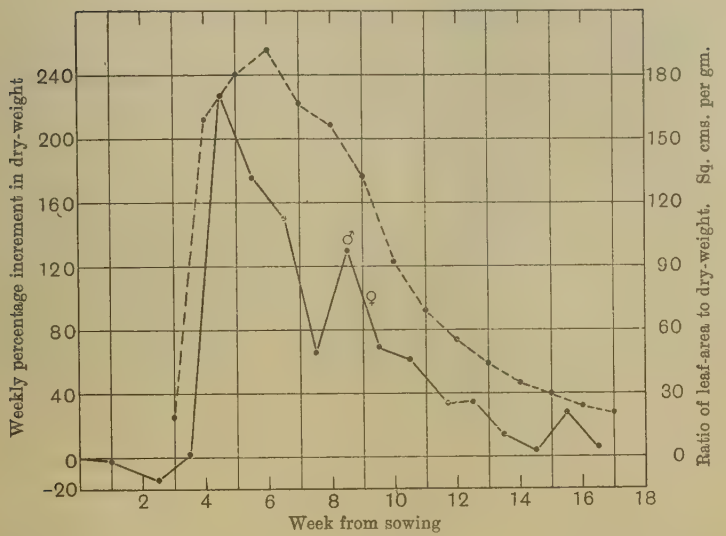
"Badischer Früh" maize 1875 —— Growth curve ..... Leaf-area ratio curve

Fig. 4.



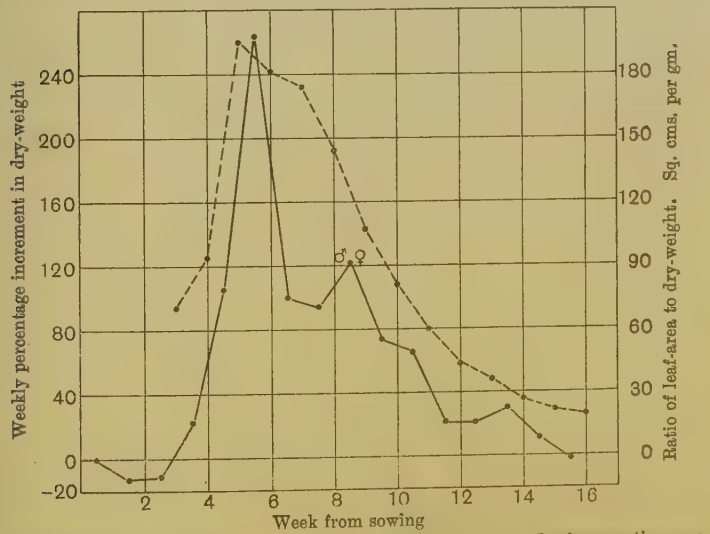
"Badischer Früh" maize 1876 —— Growth curve ..... Leaf-area ratio curve

Fig. 5.



"Badischer Früh" maize 1877 ——— Growth curve ..... Leaf-area ratio curve

Fig. 6.



"Badischer Früh" maize 1878 ——— Growth curve ..... Leaf-area ratio curve

Fig. 7.

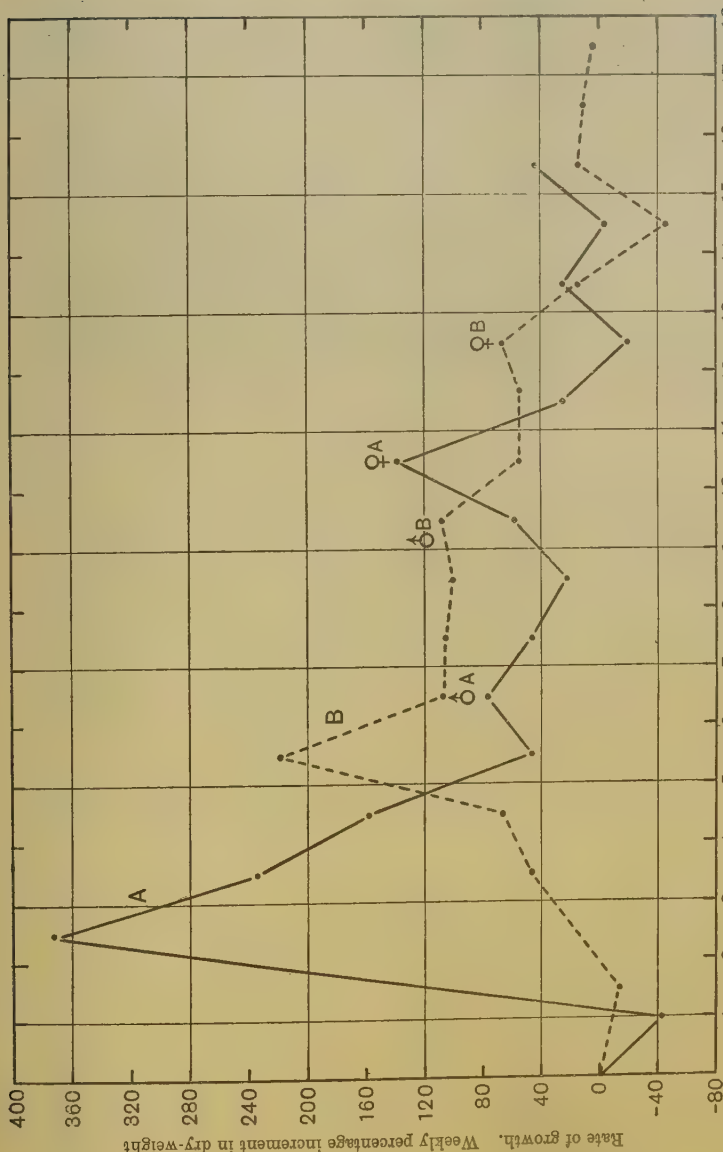
are given in Fig. 8. These results are for tops only, not for the entire plant, including roots, as in the other cases.

It is striking that when there is only one prominent subsidiary maximum the male and female flowers appear together. These subsidiary maxima cannot be correlated with recorded variations in any climatic conditions and consequently it seems safe to conclude that they must be due to internal changes.

In endeavouring to explain these maxima and their correlation with the appearance of the male and female flowers in terms of assimilation and respiration there are two alternatives. The first is to suppose that at the recorded time of the appearance of the flowers there is a temporary increase in assimilation per unit leaf-area or a decrease in respiration per unit dry-weight, or a temporary increase in salt absorption by the roots. The other alternative is to suppose that during the early stages of flower development, prior to the first record, the reverse conditions obtain, in other words, that the minima immediately preceding the record of the appearance of flowers is to be attributed to these reverse conditions. Since it is a well-known fact that flower development is accompanied by an increased respiratory activity and also since we have no evidence that there is an alteration in assimilation per unit leaf-area connected with flower-formation, the safest conclusion at present seems to be that the minima are to be correlated with increased respiratory activity at these periods.

Plants grown at the same time under similar conditions show a coincidence of the maxima (Fig. 2), but when we compare plants grown at different times and under different conditions the incidence of the maxima varies (Fig. 3). It appears likely therefore that the incidence of the maxima depends upon external conditions. As attempts to correlate the maxima with the environmental conditions obtaining at the time of their incidence were unsuccessful, we have concluded that most probably the time of the incidence of the maxima is determined by environmental conditions obtaining at previous stages in the plant's development.

Having now considered the whole of the growth-rate curve for maize it appears on the basis of the data available that the general form of the curve and the occurrence of its various maxima are controlled by internal changes intercorrelated with morphological developments. The points in morphological development which appear to be significant are (1) the rise to a maximum and the subsequent fall in the leaf-area dry-weight ratio, (2) the development of the male flowers, and (3) the development of the female flowers. Environmental conditions may influence



A. "Badischer Früh" maize (Morgen). B. "Italienische Bastard" maize (Osswald). *Tops only.*

Fig. 8.

the time relation of these points and thus the time relations of the maxima on the curve. In extreme cases the environmental factors may so far affect morphological differentiation as to cause coincidence of the maxima.

External conditions, in addition to causing modification in this way in the general form of the growth-rate curve, must directly affect the absolute value of the growth-rate, but an analysis of these curves and attempts to correlate still smaller fluctuations in these curves from year to year with external conditions have not yielded any definite results. We shall return to the subject of the effect of external conditions when dealing later with another form of expressing growth-rate, namely increase in dry-weight per unit leaf-area per unit time.

In a future chapter we propose to compare the relative growth-rate curves of other annual plants with those for maize which have been dealt with above.

Average Growth-Rate.

A full consideration of all the data presented here will show the extraordinary difficulty of finding any valid basis for comparing plants such as maize by means of their average growth-rate whether the average is taken over the whole life-cycle, which is of varying length, or whether arbitrary periods of shorter duration are taken. It is particularly misleading to compare the average growth-rate for one period of one plant with a different period of another plant. For example, a comparison of any two plants by means of their average growth-rate over a period such as six weeks would be favourable to one, whereas a comparison over say 12 weeks might be favourable to the other.

In a subsequent chapter dealing with the question of growth-rate in relation to yield, this point will receive detailed consideration.

Summary.

The series of articles of which this is the first instalment, constitutes an attempt to formulate methods for the quantitative analysis of plant growth and to apply these methods to data which have been lying dormant in the literature for 40 years.

In the present chapter the relative growth-rate curve, which is the weekly percentage increase in dry-weight plotted against time, and also the leaf-area ratio curve, that is, the leaf-area in sq. cms. per g. plotted against time, have been employed. And as a typical example of an

annual plant maize has been selected since data are given by Kreusler for this plant grown in four successive years.

The first noteworthy result of this analysis is the demonstration of the fact that the growth-rate varies greatly in magnitude at different periods in the life-cycle of a plant such as maize in a perfectly definite manner.

Fig. 9 gives the generalised form of the growth-rate curve for maize throughout its life-cycle. Although the broad form is that of a Sach's grand period curve, it must be noted that it is not a grand period curve, since the grand period curve as defined by Sachs is the curve of the actual increment per unit of time plotted against time and not of relative increment, that is, increment per unit of matter per unit of time plotted against time. On the broad form of the relative growth-rate curve

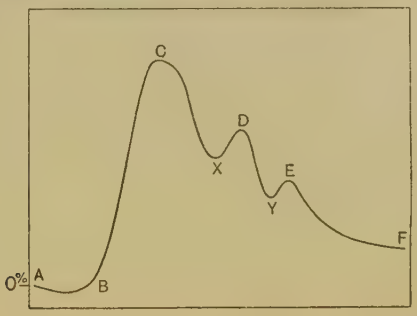


Fig. 9. Generalised form of the growth-rate curve for maize.

for maize are superposed three secondary features, an initial fall, and two subsidiary maxima on the descending limb.

In this generalised curve the initial period A–B is the period before the assimilatory organs are able to counterbalance the loss in dry-weight due to respiration, and the rate of growth is consequently negative or nil. The phase B–C corresponds to a phase in morphological development during which the leaf-area per unit dry-weight increases to a maximum. The phase C–F covers the remainder of the life-cycle of the plant during which the leaf-area per unit dry-weight is continuously decreasing. The subsidiary maxima D and E coincide with the time of the record of the appearance of the male and female flowers respectively. The minima X, Y which precede these maxima, correspond with the earliest stages of flower development, and are possibly due to increased respiration during that period.

The incidence of the maxima is controlled by environmental conditions—not by the environmental conditions operating at the time, but by those obtaining at some previous stage in the life-history of the plant.

The fact that the curve for leaf-area per unit dry-weight throughout the season (which has been calculated) shows a correspondence with the growth-rate curve indicates that the physiological basis for increased and decreased relative rate of growth is a corresponding change in the assimilating area per unit dry-weight. This point will be dealt with in the next chapter.

Evidence from the quantitative analysis of plant growth for maize indicates that the seedling leaves do not perform their normal assimilatory function till some time after their appearance.

(*To be continued.*)

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NOTES ON CHEMOTROPISM IN THE HOUSE-FLY.

By E. R. SPEYER.

The experiments described in this paper were carried out under the auspices of the Bureau of Entomology, United States Department of Agriculture, at Washington in 1914.

Acknowledgments are due to the Bureau for permission to publish these notes, and to Dr L. O. Howard, Mr W. D. Hunter, to the Bureau of Chemistry and the Institute of Chemical Research, for much valuable assistance in making the records.

In its original form, this paper embodied a Synopsis and Review of literature upon Chemotropism in Insects up to the year 1914, but it has been decided to omit these, in view of the existence of at least one publication dealing with the literature, and of other important work done by Entomologists since these notes were written.

It may be explained here that the terms Positive and Negative Chemotropism are applied respectively to substances which exert a definite attraction and a definite repulsion to the insects mentioned.

SECTION I.

PRELIMINARY EXPERIMENTS UPON THE ATTRACTION OF THE HOUSE-FLY BY COMMON FOOD-STUFFS.

(*a*) *Type of trap used.*

In all these and future experiments here described, the No. 1 Galvanized "Perfect" Fly-Trap (to be obtained from the Ludlow-Saylor Wire Co., St Louis, Missouri) was employed. It is about 2 feet 6 inches high, 8 inches in diameter at base, composed of wire gauze supported by three metal strips, and fitted with a metal lid. At the base of the trap is an inverted wire cone with a rim of supporting metal. This rim fits closely within a corresponding ring on the outside wire, to which it can be fixed by means of three screws. At the top of the cone is a small hole which admits the insects into the trap. The bait is placed in a dish beneath the wire cone.

(*b*) *Collection of insects from the traps.*

After an experiment the insects contained in the traps were killed by the emersion of the whole trap in hydrocyanic acid gas, generated from potassium cyanide and sulphuric acid (dil.) in a small crucible placed at the bottom of a large metal vessel, used generally for the removal of manure from stables. After about two minutes exposure the insects were shaken on to a sheet of paper and collected in glass vials.

Special note was taken of any flies found dead in the traps (by careful removal of the cone) before exposure to the gas, and also of insects found dead in the bait-dishes.

(*c*) *Disposition of traps.*

In these preliminary experiments, six traps were placed upon the floor of a stable at the Government Agricultural Experiment Station near Arlington, Washington D. C., U.S.A.

In this stable were two horse-boxes where large numbers of house-flies were breeding. Six traps, A, B, C, D, E and F were used for the experiments, located as follows:—The distance between A and B, C and D, E and F, in each case was 6 inches, the distance between B and C, D and E was 10 feet respectively, and the distance from F to A 15 feet. Traps B, C and E had, for baits, various attractive substances, whilst A, D and F had, in the first series of experiments, a control substance—the same in each trap—of moderate attractive power: in the second series a control substance of great attractive power.

After a convenient interval, the traps B, C and E were interposed with their baits, so that they occupied each position for three equal periods of time, and the contents of each trap in its three positions were added together.

(*d*) *Sources of error and their compensation.*

1. Owing to the nature of the traps, a number of flies might escape from the entrance to the trap, after being attracted to a specific substance, and fly to another trap.

All the traps in an experiment would be affected to a similar degree, so that the error is of little magnitude.

2. The position of some traps was certainly more favourable than that of others, apart from the power of the attractive substances used in them.

This was fully compensated for by the interposition of the traps described under (*c*).

3. A different temperature over any one period of time from that of another would have the effect of influencing the number of flies attracted to traps placed in the most favourable positions.

This error, which could not be rectified, is the only one to be considered, and it is very unlikely that the figures given were affected to anything but a negligible degree.

Experiment 1. *Common food-stuffs.*

Date:—August 27th–29th.
General weather conditions:—Dull, cool at start.
Bright, hot at finish.
Duration of experiment:—90 hours.

Exp.	Substance	Amount	Flies caught ♂	♀	Total	Control substance		Flies caught ♂	♀	Total
1	Banana	½ crushed in dish	456	715	1171*	Brown sugar and water		20	25	45
2	Vanilla extract in 61 % alcohol	30 c.c.	111	229	340†	„	„	8	9	17
3	Acetic acid (glacial)	30 c.c.	2	4	6	„	„	1	10	11

* Includes 147 ♂♂ and 204 ♀♀ found dead in traps.
† Includes 15 ♂♂ and 17 ♀♀ found dead in trap and 74 flies found dead in liquid.

Experiment 2. *Common food-stuffs.*

Date:—August 31st–September 1st.
General weather conditions:—Bright, hot.
Duration of experiment:—Experiment substances, 48 hours.
Control substances, 24 hours.

Exp.	Substance	Amount	Flies caught ♂	♀	Total	Control substance	Amount	Flies caught ♂	♀	Total
1	Vanilla extract (ordinary)	20 c.c.	17	27	44*	Grape juice	10 c.c.	49	55	104
2	Lemon extract	25 c.c.	2	10	12	„ „	10 c.c.	3	4	7
3	Spirit of vinegar	25 c.c.	3	5	8	„ „	10 c.c.	22	51	73

* Including 2 found dead in trap and 3 flies dead in liquid. Five flies found dead in grape juice. Control substances were only used during the second 24 hours of this experiment.

In these experiments the "Amount" given denotes the total quantity of the substance used for the three interpositions: at the end of each interval of time the substances were renewed.

The figures show that banana is the most attractive substance, grape juice, vanilla extract, lemon extract, brown sugar and water, spirit of vinegar and glacial acetic acid following in order.

The strong grape juice controls in Exp. 2 attracted the flies away from the vanilla extract and lemon extract: this is shown by the fact

that, during the first 24 hours, while no controls were used, the figures for the experiment substances were vanilla extract 25, lemon extract 12, spirit of vinegar 3.

It may be well here to give the results of these two experiments in percentages, to give an idea of the proportion of flies out of 100 which would enter each trap.

Experiment 1		*Experiment* 2	
Banana	74	Grape juice	66
Vanilla extract	21	Vanilla extract	24
Brown sugar and water	4	Lemon extract	6
Acetic acid (glacial)	1	Spirit of vinegar	4
	100		100

The figures for the controls are, of course, derived by calculation, allowance being made for the three traps instead of one in each case, and for the duration of time in the second case. In both cases the position of vanilla extract appears to be approximately the same, showing that the figures are reliable.

It may be added that the number of flies caught in the weak controls in Exp. 1 are in a rough direct proportion to their experiment substances, so that it would appear that they had, themselves, a definite attraction to the flies brought into their proximity by the strongly attractive agents, and doubtless had the effect of compensating for the error due to flies leaving an experiment substance and flying to another.

Experiment 3. *The increase in attraction of banana due to fermentation and decomposition.*

Date:—August 28th–September 2nd.
General weather conditions:—Du'l and cool during first period.
Hot and bright after.
Total duration of experiment:—138 hours.

Period	Duration	Flies alive in trap			Flies dead in trap			Total flies caught		
		♂	♀	Total	♂	♀	Total	♂	♀	Total
1	23 hours	33	75	108	0	1	1	33	76	109
2	43 ,,	191	192	383	147	203	350	338	395	733
3	24 ,,	—	—	—	—	—	—	49	68	117
4	24 ,,	4	28	32	12	21	33	16	49	65
5	24 ,,	0	0	0	0	0	0	0	0	0

By an unfortunate oversight, the numbers of flies found dead, and of those found alive in the trap were not differentiated during Period 3.

The positively chemotropic stimulus in banana and in grape juice is due to products of fermentation. To prove this beyond doubt a fresh

banana was pealed and cut into two halves. One half was crushed into a glass dish and set under a trap.

However, it is clearly seen that, during decomposition, banana becomes increasingly attractive, and the attractive power passes off as the putrescent mass dries off. The banana used was rather overripe at the start, and the results of Exp. 5 in Section II prove that the attractive qualities are exceedingly small when the fruit is rather unripe, an increase in the numbers being again shown when decomposition has set in, in Exp. 6.

It will have been observed that, not only with banana, but also with vanilla extract as baits, there is a high percentage of mortality amongst both male and female flies after they have entered the traps, and an increasing mortality as decomposition proceeds in banana.

This cannot be attributed to the fact that the flies were at the extreme limits of their life-existence, for a very large proportion of the female flies contained eggs, and it is clear to a degree that, in the case of banana, the decomposition and fermentation products have a deleterious effect just as strong oil of citronella has upon Dacus (Howlett)[1].

It does not imply, however, that the decomposition products are a stimulus to oviposition, for the flies were directly attracted away from manure, where they were breeding, though it must be admitted that some reagents in banana and manure may be similar in composition as an enticement to breeding. The mortality in vanilla extract is evidently attributable to alcoholic evaporation. The large proportion in many cases of female to male flies is merely due to the fact that the former were most abundant in the locality.

With regard to the attractive features of glacial acetic acid and spirit of vinegar, these substances might be found to have increased stimulating powers when diluted to an optimum solution (see Barrows)[2]. The latter reagents also produce mortality to a slight degree, grape juice, when fermenting to a considerable degree, and reference is here made to experiments with alcohols, aldehydes and acids described in Section II, proving that this is due to the products of alcoholic, aldehydic and acidic fermentation of organic substances.

Banana, as being the most attractive substance to the house-fly, is used as the basis of investigation in the next section.

[1] *Trans. Ent. Soc. Lond.* Part II, pp. 412–418.

[2] *Journ. Exp. Zoology*, Baltimore, Md. pp. 515–537.

SECTION II.

EXPERIMENTS WITH THE DECOMPOSITION PRODUCTS OF BANANA AND SUBSTANCES ALLIED TO THEM.

It is possible to deduce the approximate composition of banana from E. Munroe Bailey's "Studies on the Banana," *Journal of Biological Chemistry*, I. 1, p. 355.

Ripe Banana.

	%	%	
Solids	21·5–34·5		Water difference from 100.
Protein	0·6– 2·1		
Invert sugar	3·1–21·4	}	When invert high, cane low and *vice versa*.
Cane sugar	0·2–17·5	}	
Total sugar	12·3–25·6		
Other nitrogen free extract	2·0–10·7		
Fibre	0·2– 1·2		
Ash	0·7– 1·1		

Unripe Banana.

Unripe banana contains insoluble carbohydrates, which, in the presence of air, give place to soluble carbohydrates when the fruit ripens.

Thus the proportion of soluble and insoluble carbohydrates as *dextrose* is

	Soluble	Insoluble	Total
In unripe banana	1·3	25·2	26·5
In ripe banana	17·1	1·9	19·0

The decomposition products therefore contain few nitrogen compounds, and ferment to the decomposition products of carbohydrates, such as alcohols, acids and their compounds.

The method of experiment adopted was similar to that in Section I, but the traps were placed in a glass house on a table 4 feet from the ground and in a straight line. Instead of employing control substances, each pair of traps was baited with a known quantity of the same substance.

The distance between each pair of traps was about 4 feet, those containing similar substances being placed 6 inches apart. The pairs were interposed as in the previous experiments.

The first series was carried out to determine the general qualities of carbohydrates in an unfermenting condition. For the purpose, brown sugar, white sugar, and starch were used in a dry condition; water was

intentionally not added to them, as moist substances always show a certain attraction, when not actually repellant, on account of the water contained by them.

Experiment 4. *Carbohydrates.*

Date:—September 10th–12th.
General weather conditions:—Cool, rain.
Duration of experiment:—69 hours.

Substance	Amount oz.	Flies caught ♂	♀	Total	Percentage
Brown sugar	4	4	6	10	84
White sugar	4	0	0	0	0
Starch	4	1	1	2	16
					100

In spite of the small numbers caught, there was an abundance of flies round the traps, and the results show that carbohydrates in this condition are very moderately attractive.

The odour of banana is strongly reminiscent of amyl acetate, and minute quantities of the latter substance suggest that amyl compounds might well be derived from ripening and decomposition products through fermentation.

Experiments were accordingly carried out to test the attractiveness of these substances, relating to each other and to decomposing banana.

They bear the formulae: amyl alcohol, $CH_3(CH_2)_4OH$; amyl acetate, $CH_3(CH_2)_4CH_2COOH$; valerianic aldehyde, $CH_3(CH_2)_3CHO$; valerianic acid, $CH_3(CH_2)_3COOH$.

Though closely allied, the odours which they give off are very different, the acid being especially pungent.

Valerianic aldehyde took some time to prepare in the laboratory, and was therefore not available for experiment until later.

In the first of the two following experiments, an unripe pealed banana was used: this was afterwards crushed and allowed to ferment in a covered glass vessel for four days, at the end of which time it was used for the second experiment. The liquids were used in a pure, undiluted state in all subsequent experiments.

This at once points to the fact that, whilst unripe and not decomposed banana is very much less attractive than amyl alcohol and amyl acetate, on decomposition it becomes more attractive than amyl acetate and valerianic acid. The figures in Exp. 6 give no idea of the relative strengths of amyl acetate and valerianic acid, as the former substance

held the most favourable position, the short duration of the experiment, for obvious reasons, preventing interposition of the traps.

Experiment 5. *Decomposition products of banana.*

Date:—September 30th–October 1st.
General weather conditions:—Bright, warm.
Duration of experiment:—44 hours.

Substance	Amount c.c.	Flies caught ♂	♀	Total	Percentage
Amyl alcohol	60*	5	4	9	41
Amyl acetate	60*	4	8	12	54
Banana (unripe)	—	1	0	1	5
					100

* Denotes 20 c.c. for each period.
Five flies were found dead in the amyl acetate trap.

Experiment 6. *Decomposition products of banana.*

Date:—October 5th–6th.
General weather conditions:—Warm, dull.
Duration of experiment:—24 hours.

Substance	Amount c.c.	Flies caught ♂	♀	Total	Percentage
Amyl acetate	20	14	18	32	39
Valerianic acid	20	11	5	16	19
Banana (decomposed 4 days)		18	17	35	42
					100

Two flies were found dead in the valerianic acid trap.

Experiment 7.

Date:—October 2nd–3rd.
General weather conditions:—Bright, warm. At termination, cool with some rain.
Duration of experiment:—69 hours.

Substance	Amount c.c.	Flies caught ♂	♀	Total	Percentage
Amyl alcohol	28	1	6	7	7
Amyl acetate	28	5	15	20	19
Valerianic acid	28	27	51	78	74
					100

Three flies found dead in amyl acetate, 6 in amyl alcohol, and 12 in valerianic acid traps.

Here are shown the relative attractive powers of these three liquids, and it is seen that they fall into the order in which one would expect

them to be formed during fermentation, with increased positive chemotropic effects.

After October 5th the flies unfortunately became lethargic, and the following figures suffer very much from the insects being in this condition.

It is therefore not possible to determine the exact position of valerianic aldehyde in relation to the above reagents. Exp. 9 shows it to be strongly attractive under the prevailing conditions, but does not give an idea as to its holding a place between amyl acetate and valerianic acid, which, on the face of what has gone before, is quite probable.

To come to some conclusion as to what arrangement of molecular grouping furnishes these substances with their positive chemotropic powers, records were taken of the numbers of flies caught respectively by four alcohols, three aldehydes, and three acids—as here named with their chemical formulae:

Methyl alcohol, $H.CH_2OH$; ethyl alcohol, CH_3CH_2OH; amyl alcohol, $CH_3(CH_2)_3CH_2OH$; benzyl alcohol, $C_6H_5.CH_2OH$.

Valerianic aldehyde, $CH_3(CH_2)_3CHO$; benzaldehyde, C_6H_5CHO; cinnamaldehyde, $C_6H_5(CH)_2CHO$.

Valerianic acid $CH_3(-CH_2)_3COOH$; benzoic acid + ethyl alcohol, $C_6H_5.COOH + CH_3CH_2OH$; cinnamic acid + ethyl alcohol, $C_6H_5(CH)_2COOH + CH_3CH_2OH$.

All these were used undiluted, except for the two solids benzoic acid and cinnamic acid, of which saturated solutions were prepared in pure ethyl alcohol.

Experiment 8. *Alcohols.*

Date:—October 6th–7th.
General weather conditions:—Warm, dull.
Duration of experiment:—23 hours.

Substance	Amount c.c.	Flies caught ♂	♀	Total
Methy alcohol	20	0	0	0
Ethyl alcohol	20	1	2	3
Amyl alcohol	20	0	1	1
Benzyl alcohol	20	0	1	1

Percentages are not given, as the number of the flies caught is insufficient. The only fly caught by benzyl alcohol probably entered the trap by accident.

Ethyl and amyl alcohols are the only two attractive ones.

Experiment 9.

Date:—October 7th–9th.
General weather conditions:—Warm, dull.
Duration of experiment:—45 hours.

Substance	Amount c.c.	Flies caught ♂	♀	Total
Valerianic aldehyde	20	3	6	9
Benzaldehyde	40	0	3	3
Cinnamaldehyde	40	1	0	1

Experiments with oil of bitter almonds point to the fact that benzaldehyde is not positively chemotropic, and the same applies to cinnamaldehyde.

Experiment 10. *Acids.*

Date:—October 6th–9th.
General weather conditions:—Warm, dull.
Duration of experiment:—69 hours.

Substance	Amount c.c.	Flies caught ♂	♀	Total	Percentage
Valerianic acid	20	17	28	45	71
Benzoic acid in 100 % ethyl alcohol	45	9	7	16	26
Cinnamic acid in 100 % ethyl alcohol	70	1	1	2	3
					100

The last figures are more satisfactory, and give valerianic acid a percentage close to that of Exp. 7 when this liquid was used in company with an alcohol and an acetate. From observations made upon solid benzoic and cinnamic acids it is probable that these substances owed their attractive features solely to the ethyl alcohol in which they were dissolved, and benzoic acid may actually be negatively chemotropic.

A curious observation was made upon flies exposed to cinnamic acid, in that they show a prolonged immunity to the fumes of hydrocyanic acid gas. The effect of cinnamic acid is therefore probably antidotal to the insects.

The conclusions to be drawn are as follows:

1. Saturated alcohols, aldehydes and acids are positively chemotropic in products of fermentation, as far as amyl compounds are concerned.

2. Alcohols, aldehydes and acids containing the methyl group CH_3 are positively chemotropic, except in cases where their molecular weight is about 30 (methyl alcohol) or below, the chemotropic stimulus being

aggravated where the methyl group is augmented by union with $(CH_2)_x$.

3. Compounds containing the benzene ring are unattractive though not necessarily negative. These are unsaturated.

4. Amyl compounds are probably increasingly attractive in the order in which they are formed during fermentation and decomposition.

5. If, in this series, valerianic aldehyde is less attractive than amyl acetate or amyl alcohol, then it is probable that the aldehyde group, in all compounds containing it, is to a certain extent negatively chemotropic.

There is evidently no relation between volatility and chemotropic action.

Note was made of the rates of evaporation during the experiments, and these are given below, the substances being arranged in order of assumed attractive power.

	Substance	Original amount c.c.	Final amount c.c.	Loss in volume c.c.	Time hours
1	Valerianic acid	20	19	1	23
2	Valerianic aldehyde	20	7·5	12·5	23
3	Amyl acetate	20	14	6	24
4	Amyl alcohol	20	16	4	23
5	Ethyl alcohol	20	0 (water)	20	23
6	Cinnamic acid in ethyl alcohol	20	Crystalline	—	23
7	Benzyl alcohol	20	19	1	23
8	Benzaldehyde	20	Crystalline	—	22
9	Methyl alcohol	20	0 (water)	20	23
10	Cinnamaldehyde	20	20	0	23
11	Benzoic acid in ethyl alcohol	20	Crystalline	—	23

It is sufficient at this stage to point out that saturated compounds contained in fermenting vegetable substances and containing the molecular group $CH_3(CH_2)_x$ may constitute the source by which the house-fly is guided to its food.

SECTION III.

ESSENTIAL OILS.

The experiments in this section were carried out under the same conditions as those in the last.

To give an idea of the number of house-flies caught by the traps in their respective positions, a control record was taken with a known quantity of grape juice. The results were as follows:

Experiment 11. *Control with grape juice.*

Date:—September 8th–10th.
General weather conditions:—Cool, some rain.
Duration of experiment:—48 hours.

Trap	Substance	Amount c.c.	Flies caught ♂	♀	Total
A	Grape juice	20	14	17	31
A′	„ „	20	32	28	60
B	„ „	20	44	23	67
B′	„ „	20	6	13	19
C	„ „	20	9	2	11
C′	„ „	20	12	12	24

The average for each pair of traps (A, A′; B, B′; C, C′) is, then, about 70 flies for the 48 hours. Traps B and A′ are seen to be in the most favourable positions, and the pairs A, A′ and B, B′ are credited with the highest number. By interposition the differences are eliminated in the following experiments.

It might be thought that many of the sweet-smelling essential oils are attractive to the house-fly, but this is here shown to be a misconception, for many of them are, to a certain degree, actually repellent.

Experiment 12.

Date:—September 15th–18th.
General weather conditions:—Warm, bright.
Duration of experiment:—76 hours.

Substance	Amount c.c.	Flies caught ♂	♀	Total
Cedar oil	20	0	0	0
Oil of juniper berries	20	0	1	1
Oil of *Pinus Sylvestris*	20	0	0	0

At the same time, three traps were placed in the stable used for the experiments in Section I for 26 hours. The figures were exactly similar to the above, and in both cases the female fly in the juniper oil trap was dead. It is probable that the two flies entered by accident.

Experiment 13.

Date:—September 18th–21st.
General weather conditions:—Warm, bright.
Duration of experiment:—46 hours.

Substance	Amount c.c.	Flies caught ♂	♀	Total
Orange oil	20	0	1	1
Lemon oil	20	0	0	0
Citronella oil	20	0	1	1
Camphor oil	20	0	0	0
Clove oil	20	0	0	0
Eucalyptus oil	20	0	0	0

Here again the oils are seen to be almost totally unattractive. The stray insects which enter the traps do so merely by accident.

Eucalyptus oil is said to contain valerianic acid, and it is noteworthy that no flies were attracted to it.

It has been demonstrated that these essential oils are unattractive but it still remains to be shown if any of them are actually repellent, i.e. negatively chemotropic.

For this purpose, the traps were used in the same positions as before, but under each were placed two dishes—one containing a known quantity of an essential oil, and the other a known quantity of grape juice.

At the end of each period of time the traps were changed as to their positions, a new supply of grape juice being used for each period, and the oils being left to evaporate through the whole time.

This was done particularly to avoid fermentation of the grape juice, and total evaporation, for the amount of alcohol formed in the fermenting liquid volatilises at a high speed, leaving behind carbohydrates in the form of sugar.

Experiment 14. *Repulsion by essential oils.*

Date:—September 21st–24th.
General weather conditions:—Very hot, storms at termination.
Total duration of experiment:—72 hours.

	Substance	Amount at start c.c.	Amount at finish	Flies caught: Period 1, 24 hours ♂	♀	Total	Period 2, 24 hours ♂	♀	Total	Period 3, 24 hours ♂	♀	Total
1	Lemon oil	14	0·75 c.c. renewed at each period	0	1	1	0	0	0	251	240	491
	Grape juice	30										
2	Orange oil	14	1·0 c.c. renewed at each period	0	0	0	12	9	21	43	52	95
	Grape juice	30										
3	Citronella oil	14	4·0 c.c. renewed at each period	1	1	2	0	0	0	45	69	114
	Grape juice	30										

It would appear that, although strongly repellent at first, these oils lose their repellent properties with evaporation, and further that the attractive qualities of grape juice emanate through the oils, thus approximating insects to the traps, into which they rush in great numbers when the repellent properties disappear.

An experiment made shortly after, substituting camphor oil for

citronella oil, and cedar oil for lemon oil, bears this out. Flies were still abundant round the traps.

Experiment 15. *Repulsion by essential oils.*

Date:—September 26th–28th.
General weather conditions:—Cool, bright.
Duration of experiment:—42 hours.

	Substance	Amount at start c.c.	Amount at finish c.c.	Flies caught ♂	♀	Total
1	Orange oil	14	6·5	14	6	20
	Grape juice	30	—			
2	Camphor oil	14	3·0	0	1	1
	Grape juice	30	—			
3	Cedar oil	14	11·0	13	9	22
	Grape juice	30	—			

It must be remembered that these figures are comparable to the first two periods of Exp. 14, and orange oil holds the same place in both cases.

The latter oil appears to lose its repellent power sooner than lemon oil and citronella oil.

Experiment 16. *Repulsion by essential oils.*

Date:—September 25th–26th.
General weather conditions:—Cool, bright.
Duration of experiment:—27 hours.

	Substance	Amount at start c.c.	Amount at finish	Flies caught ♂	♀	Total
1	Camphor oil	14	6·0 c.c.	34	22	56
	Grape juice	30	—			
2	Eucalyptus oil	14	6·0 c.c.	32	29	61
	Grape juice	30	—			
3	Oil of bitter almonds	14	Crystalline	99	90	189
	Grape juice	30	—			

None of these can be truly repellent except camphor oil, and traps set alone with oil of bitter almonds, a substance with a smell resembling benzaldehyde, show that the latter is certainly not attractive. The same has also been demonstrated with cedar oil and eucalyptus oil. The high figures for camphor oil were no doubt due to the enormous numbers of flies round the traps, and another experiment was made to certify this.

Experiment 17. *Repulsion by essential oils.*

Date:—September 28th–30th.
General weather conditions:—Bright, cool.
Total duration of experiment:—45 hours.

	Substance	Amount at start c.c.	Amount at finish	Flies caught: Period 1, 22 hours ♂	♀	Total	Period 2, 23 hours ♂	♀	Total
1	Camphor oil Grape juice	14 20	1 c.c. renewed at each period	0	1	1	1	0	1
2	Cedar oil Grape juice	14 20	13 c.c. renewed at each period	1	4	5	7	1	8
3	Oil of *Pinus Sylvestris* Grape juice	14 20	3·5 c.c. renewed at each period	1	0	1	0	0	0

The author wishes to make it clear that he does not consider the experiments upon actual repulsion by essential oils in any way final until further observations are made in a similar direction. This applies to eucalyptus and camphor oils, two substances of almost indistinguishable odour when in the pure state, in special.

Weather conditions may have much to do in determining the repellent qualities when placed in juxtaposition with attractive substances, and when flies are in great numbers, it is not impossible that they should invade, to them malodorous compounds, to reach positively chemotropic reagents.

The conclusions drawn, then, are subject to revision.

1. Essential oils are unattractive to the house-fly in general.

2. Certain essential oils evoke negatively chemotropic stimuli, these being oil of *Pinus Sylvestris*, orange oil, lemon oil, citronella oil, oil of juniper berries, and possibly camphor oil.

3. Certain essential oils are inactive in raising stimuli, these being cedar oil, eucalyptus oil, and oil of bitter almonds. They may themselves be neither positively, nor negatively, chemotropic in action, but probably have slight negative features.

4. During evaporation, the repellent actions pass off, soonest in orange oil and later in lemon oil, citronella oil, and oil of *Pinus Sylvestris*, and some coordination may occur in relation to the rate of evaporation and the retention of repellent qualities.

Note:—Essential oils are not repellent to all insects. Gryllidae were repeatedly found in camphor, lemon, citronella oils; also some Diptera

of the Genus *Culex* (though oil of citronella is strongly repulsive to these), and Lepidoptera of the families *Noctuidae* and *Geometridae*.

A single *Stomoxys calcitrans* Linn. was found in oil of juniper berries, and one *Calliphora irridescens* Des.

Citronella oil has already been mentioned as attracting two species of Dacus, and oil of bitter almonds attracts species of Thrips (Howlett)[1].

On September 23rd, the traps baited with orange oil and grape juice contained 3 dead male flies and 1 dead female out of a total of 12 males and 9 females.

On September 24th 4 flies were floating in lemon oil used in conjunction with grape juice out of a total of 251 males and 240 females.

In both instances these may have fallen into the oil dishes by accident after feeding heavily on the grape juice.

SECTION IV.

RECORD OF OTHER INSECTS OBSERVED DURING THE EXPERIMENTS.

The following table gives a record of Diptera attracted to substances used in the various experiments of Sections II and III, but it must be remembered that the traps employed were not suitable for the collection of many of the smaller species, of which a considerable number must have escaped.

The various re-agents are designated by letters, as below:

A, Amyl alcohol; B, Amyl acetate; C, Valerianic aldehyde; D, Valerianic acid; E, Cinnamic aldehyde; F, Cinnamic acid in ethyl alcohol; G, Oil of bitter almonds; H, Oil of juniper berries; I, Grape juice; J, Banana; K, Brown sugar. The numerals represent the number of insects attracted to that particular bait.

Muscina stabulans Fall. E 1, F 3, I 10, J 3: total 17. *Sarcophaga assidua* Walk. D 3, I 15, J 1: total 19. *Sarcophaga helicis* Town. B 1, I 1: total 2. *Fannia canicularis* Linn. A 3, D 1, F 1, G 1, I 3, J 7: total 16. *Drosophila ampelophila* Loew. A 1, B 2, I 2: total 5. *Stomoxys calcitrans* Linn. A 2, H 1: total 3. *Calliphora irridescens* Des. G 1. *Calliphora erythrocephala* Meig. I 2. *Lucilia caesar* Linn. I 2. *Lucilia sericata* Meig. I 1. *Phormia regina* Meig. I 1. *Phorbia fusciceps* Leff. D 1. *Limosina* sp. B 2. *Borboridae* A 4, D 2: total 6. *Spilogaster* sp. K 1. *Chironomus* sp. B 1. *Boetechenia latisterna* Pack. I 1. *Cynomia cadaverina* Des. J 1.

It is noticeable that only one fly, *Fannia canicularis* Linn., was attracted to a substance containing the benzene ring as well as to substances containing the $CH_3.CH_2$ group, and, in the case of the former, only one fly was found in each trap. On the other hand, *Muscina stabulans* Fall. occurred only in substances containing the benzene ring.

[1] *Journal of Economic Biology*, Vol. IX, No. 1, pp. 21–23.

Sarcophaga assidua Walk. was a common insect at the time, and was attracted to valerianic acid, grape juice, and banana only. Howlett has observed that other species of *Sarcophaga* are strongly influenced by a solution of Skatol, which contains the benzene ring and a methyl group. This substance is found in faeces. Its effect upon *Sarcophaga* seems to be to guide the female to places for oviposition. It may be that the benzene ring reacts positively to fertile females, and products of fermentation to individuals generally as a guide to food only.

Amongst the other insects caught in these experiments, the Coleoptera, *Epitrix parvula* Fab., and *Chaetocnema denticulata* Illiger, occurred in valerianic aldehyde and amyl acetate respectively—one specimen of each.

Gryllidae were often found in traps baited with essential oils, namely, citronella, lemon, and camphor oil: also in traps baited with amyl alcohol and methyl alcohol, but in the latter cases seldom more than one in each trap.

Thysaneura of the Genus *Lepidocyrtus*, and, on Mr Banks' authority, closely allied to, but distinct from *L. metallicus*, were attracted in some numbers to amyl acetate, valerianic acid, and amyl alcohol. These insects were not influenced by benzaldehyde or cinnamic acid.

Finally, it is not considered that the *Valerianic* series of substances is necessarily the series acting most positively to the house-fly, and it is suggested that experiments be carried out with the *Butyric* series.